# ECOLOGICAL ENERGETICS OF CALIDRIDINE SANDPIPERS BREEDING IN NORTHERN ALASKA

A

DISSERTATION

Presented to the Faculty of the

University of Alaska in Partial Fulfillment

of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

David W. Norton, A.B., M.S.

Fairbanks, Alaska

May 1973

ECOLOGICAL ENERGETICS OF CALIDRIDINE SANDPIPERS

BREEDING IN NORTHERN ALASKA

APPROVED

Chairman

Vice President for Research and Advanced Study

28 March 1973
Date

ABSTRACT

Estimates are derived of annual requirements for tundra resources of four congeneric and sympatric sandpipers that breed at Barrow, Alaska, and depend entirely on a tundra arthropod fauna of limited diversity. All four species -- the Dunlin (Calidris alpina), Baird's Sandpiper (C. bairdii), Pectoral Sandpiper (C. melanotos), and Semipalmated Sandpiper (C. pusilla) -- face the same general energetic problems inherent in arctic breeding by birds. They differ, however, in temporal and spatial patterns of abundance and resource use during the breeding season, in body size, in breeding success, and in other characteristics that influence the population energy requirements. The form used in deriving estimated resource requirements follows the general assumption that (numbers of individuals) X (individual energy requirements) = total resource dependence.

The successive steps used in deriving total estimated requirements are, by chapter, estimations of: numbers and density of residence on the tundra; temporal organization of nesting effort; metabolic performance of adults; metabolic requirements of chicks; and the synthesis of this information to express total requirements, and to explore such understanding of the dynamic interactive aspects of the strategy of arctic insectivory as these estimates may afford.

ECOLOGICAL ENERGETICS OF CALIDRIDINE SANDPIPERS

BREEDING IN NORTHERN ALASKA

(Order No. )

David W. Norton, Ph.D.

University of Alaska, 1973

Supervisor: George C. West

The interactions with physical and biotic features of the tundra ecosystem, shown by populations of four congeneric and sympatrically breeding sandpipers, are explored in a five-part energetics study. The Dunlin (Calidris alpina), Baird's Sandpiper (C. bairdii), Pectoral Sandpiper (C. melanotos), and Semipalmated Sandpiper (C. pusilla) all breed at Barrow, Alaska, and depend entirely on an arthropod fauna of limited diversity, during the energy-demanding breeding cycle. All confront the same general problems inherent in arctic breeding but differ in body size, spatial and temporal patterns of resource use, and other characteristics that affect individual and population energy requirements.

Breeding densities, phenology, mating systems, and predation upon each species are documented, such that the annual tundra residency of each can be expressed as adult bird x days/ha. C. alpina, through its stable nesting densities and persistent residence on the tundra avails itself of the major share of tundra resources that shorebirds require at Barrow. Banding studies indicate that C. bairdii is anomalous in its breeding system, as the Barrow birds show elements of opportunism (lack of site attachment and mate-faithfulness between

years) despite the species' monogamous mating system.

Incubation studies document the scheduling of nest attendance---95-98% in the two-sex incubation systems of alpina, bairdii, and pusilla, and 85.5% by female melanotos, which incubate alone. Minimal and intermittent incubation during both onset and termination of incubation is credited with maximizing the within-clutch synchrony of hatching. Diurnal variations in constancy of incubation generally afford maximum protection of the eggs during the coldest hours of the day.

Metabolic performance of adult sandpipers, assessed by closed system respirometry, showed all adults to be expending energy continuously in thermoregulation at ambient temperatures normally encountered at Barrow. Resting metabolic rates of productively active birds require careful interpretation in reference to more rigorously defined metabolic parameters. Resting metabolism was maximum at the beginning and end of the incubation period. The energy budget for the nesting period indicates that incubation requires 20-35% of potential productive energy of each incubating adult. Limitation on the rates at which these birds can mobilize energy may explain avoidance of simultaneous engagement in several energy-demanding events of the breeding cycle.

Growth, bioenergetics, and thermoregulation of sandpiper chicks were studied in laboratory-reared and wild young. Hatchlings are ineffective thermoregulators at temperatures near 0°C, and operate as heterotherms when not being brooded. They remain functional and

active during periods of foraging for small insects, although their body temperatures commonly drop to 30°C, even when nearly fledged. The metabolic economy of persistent thermolability is estimated to reduce total energy requirements of chicks by some 10%. Growth was strongly affected by ambient temperatures, being optimal at warmer than average temperatures for Barrow, but suppressed above and below about 10-15°C.

Numbers of birds, their allotment of time in various activities, and their metabolic requirements are combined to estimate total energy required by each species and by the community as a whole. The total Calidris requirement approximates 4,000 kcal per ha. This value can be used in conjunction with our knowledge of arthropod biology at Barrow to derive some intriguing generalizations about arctic insectivory. Calidridine sandpipers are estimated, for example, to require 4-15% of larval arthropod biomass present, and at least 20% of the surface-active adult insects emerging annually. The required rate of prey capture is estimated as a function of the mean prey item size, time available for foraging, and daily energy requirement. Suggestions are made for verifying or amending the estimated prey requirements in subsequent field studies.

ACKNOWLEDGEMENTS

This research was supported variously by: a National Institute of Health predoctoral traineeship through the Institute of Arctic Biology, University of Alaska; the Tundra Biome Program (International Biological Program) through the National Science Foundation; the Arctic Institute of North America under contractual arrangement with the Office of Naval Research; the Department of Biological Sciences, University of Alaska. Logistical support for field research was provided by the Naval Arctic Research Laboratory.

Credit for ideas, concepts and techniques developed in this study belongs largely to my privileged associations with the following persons: my professors, George C. West, Laurence Irving, and Stephen F. MacLean, Jr.; a colleague for four field seasons, Uriel N. Safriel, who graciously allowed use of some of his conclusions concerning C. pusilla; a predecessor in Calidris studies, Richard T. Holmes, who provided data and conclusions in correspondence; and finally, Professor Frank A. Pitelka, who recognized in 1951 the importance of Barrow's Calidris sandpipers to ecological theory, and who continues to encourage investigations of all aspects of their biology. Additionally, I thank my series of able field assistants: Mark W. Oberle, Bjørnulf Kristiansen, Stephen MacDonald, Jeffrey O. Myll, Irvin W. Ailes, and James Curatolo.

The patience and skill of Don Borchert, graphic artist, and Mrs. Helga Wilm, typist, have contributed greatly to the realization of this dissertation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

## INTRODUCTION

Localities dominated by 9-10 months of subfreezing weather annually do not seem at first glance to afford attractive breeding situations for small birds. Along Alaska's arctic coast, low temperatures persist through the brief summers, and subfreezing temperatures can recur at any time, posing problems of heat loss to such small homeotherms, their eggs, and young. The terrestrial breeding avifauna in tundra ecosystems is often dominated by shorebirds. This generalization is particularly true of Barrow, Alaska (lat 71°18'N; long 156°40'W), where 7 of 11 regularly breeding species are shorebirds (Table 1). This dissertation is a study of a group of sandpiper species that breeds successfully in such an improbable area, of the adaptations allowing their reproductive success in the tundra, and of their seasonal impact on the tundra ecosystem.

Four of the seven shorebirds in Table 1 are placed in the inclusive genus Calidris, for reasons advanced by Holmes and Pitelka (1964). They belong to the scolopacid subfamily Calidridinae, which includes 24 sandpiper species largely limited to arctic and subarctic breeding grounds (Pitelka et al, MS). An important attribute of this subfamily is the diversity of breeding systems (spacing mechanisms, mating patterns, behavioral and morphological dimorphisms, etc.) that the 24 species exemplify. Pitelka et al (MS) distinguish four types of breeding system in calidridine sandpipers: monogamy, serial polygamy, polygyny, and promiscuity. Because these types may be viewed as distinct "resource exploitation strategies", and clearly do affect the spatial and temporal

TABLE 1. Terrestrial birds regularly breeding at Barrow, Alaska.

| Species | Family | Remarks |
|---|---|---|
| Nyctea scandiaca<br>Snowy Owl | Strigidae | breed only in years of Lemmus abundance (Pitelka et al, 1955) |
| Stercorarius pomarinus<br>Pomarine Jaeger | Laridae | " " " " |
| Phalaropus fulicarius<br>Red Phalarope | Phalaropodidae | abundant[1] in most years |
| Pluvialis dominica<br>Golden Plover | Charadriidae | common[1] most years |
| Arenaria interpres<br>Ruddy Turnstone | Scolopacidae | locally common most years |
| Calidris alpina<br>Dunlin | Scolopacidae | widely abundant annually |
| Calidris bairdii<br>Baird's Sandpiper | Scolopacidae | locally abundant most years |
| Calidris melanotos<br>pectoral sandpiper | Scolopacidae | absent to widely very abund- and 0-68 nests/100 ha (Holmes, 1966a) |
| Calidris pusilla<br>Semipalmated Sandpiper | Scolopacidae | locally abundant annually |
| Calcarius lapponicus<br>Lapland Longspur | Fringillidae | widely abundant most years |
| Plectrophenax nivalis<br>Snow Bunting | Fringillidae | common annually; restricted to local availability of artificial nest sites |

[1] Scale of numerical abundance: abundant > common

allocation of a species' energy requirements during the breeding cycle, it will be appropriate to use the terminology of Pitelka et al (MS) in this study. These four breeding sytems fall into two broader categories of resource exploitation strategy. The conservative approach is typified by monogamous species with annually renewed pairbonds (mate-faithfulness), return as breeding adults to natal area (philopatry), and return to the same breeding territory in successive years (site-tenacity). The opportunistic approach takes the form of any of the other three breeding systems. In the absence of site-tenacity, mate-faithfulness and philopatry, the opportunistic species are, in a sense, "freed" to capitalize on favorable local conditions, or avoid unfavorable ones in breeding efforts during a given season (cf. Pitelka et al, MS).

Two of the four Calidris species in this study are conservative and monogamous, one is opportunistic and promiscuous, while the fourth may be an anomaly, as outlined below.

The Dunlin (Calidris alpina) is a polytypic species, represented at Barrow by the Asiatic race, sakhalina (MacLean and Holmes, 1971; Norton, 1971). This race has a classically conservative, monogamous mating system. Conservatism extends to the whole suite of breeding system characteristics, including a consistent and dispersed spacing pattern of breeding territories, participation of both adults in nesting care of young, persistent residence of males and females on the breeding grounds, philopatry, mate-faithfulness, and nest site-tenacity. The high degree of dependence upon tundra resources at Barrow is further shown by C. a. sakhalina in its early arrival, tendency to re-nest if a

nest is lost to predators early in the breeding cycle, and the inclusion of feeding areas within the territories defended during the nesting period (Holmes, 1966a). In this last characteristic, the birds which breed at Barrow differ from both C. a. schinzii of Europe (Soikkeli, 1967) and C. a. pacifica of western Alaska (Holmes, 1970).

The Semipalmated sandpiper (C. pusilla) is monotypic, and the population at Barrow is nearly as conservative in breeding system as alpina. The departure of females shortly after hatching, and the clumped distribution of small breeding territories are the only non-conservative traits of pusilla (Safriel, 1971).

Baird's sandpiper (C. bairdii) is also a monotypic species, and at the outset of this study, appeared essentially to have a conservative and monogamous breeding system at Barrow. A complete understanding of its breeding strategy eludes us, despite the efforts of several investigators who have cooperatively studied the population between 1968 and 1972. Clumped dispersal patterns, early departure of one or the other adult, annual fluctuations in breeding numbers, and the erratic rhythms of alternation of the sexes during incubation (Norton, 1972) should alert us to the possibility that bairdii is opportunistic rather than conservative in social system.

The Pectoral sandpiper (C. melanotos) is genuinely opportunistic rather than conservative, and its mating system belongs in the "promiscuous" group owing to its lack of pairbonding. Occupancy of the Barrow tundra by melanotos fluctuates between 0 and 68 nests/100ha (Holmes, 1966a; MacLean, 1969). Males take no part in incubation (Pitelka, 1959;

Norton, 1972) and leave the tundra at about the time of hatching. Philopatry, nest-site tenacity, re-nesting, and mate-faithfulness are unknown and probably absent in melanotos.

The high latitude distribution of breeding grounds of modern calidridine species suggest that the evolutionary development and diversification of breeding systems have occurred in tundra communities. The tendency of several calidridine species to breed sympatrically at many arctic localities (MacLean, 1969) further suggests that they have long shared certain physiological adaptations for securing and mobilizing energy from tundra ecosystems. These adaptations are not shared by most passerines, nor by many other groups of birds notably absent from the breeding avifauna of arctic regions (cf Holmes, 1966c).

The resource base for shorebirds at Barrow is entirely tundra arthropods, primarily larval and adult forms of dipterous insects of the families Tipulidae and Chironomidae (Holmes and Pitelka, 1968). Earlier studies of the Barrow calidridine sandpipers have examined the phenology of breeding in relation to seasonal and spatial patterns of arthropod abundance (Holmes, 1966a; Holmes and Pitelka, 1968; MacLean, 1969). The thrust of these investigations was examination of how numbers, species diversity, and reproductive success might be limited by athropod resources. A full examination, however, of food as either a proximate or an ultimate limiting factor requires estimation of energy and food requirements by individuals and populations of birds during tundra residence, such that requirements and resources may be compared.

The following series of studies culminates in estimates of seasonal

requirements by Calidris sandpipers in the Barrow ecosystem (Norton, 1973d). In the process of deriving these estimates, many of the determining variables that affect seasonal impact are examined in detail. These determining variables will be useful in the elaboration of a three-part mathematical model of the shorebird compartment, being developed for the Tundra Biome of the International Biological Program. The relative importance of, and detailed knowledge surrounding Calidris sandpipers make them a logical subject for simulation modeling of avian consumers engaged in breeding.

The trophic relationships of shorebirds at Barrow are shown schematically in Figure 1, which stresses their dependence on saprovorous insects. The shorebirds' predators shown are primarily predators on lemmings (Lemmus), and only facultatively shift to shorebird eggs and young. The shorebird compartment itself is the subject of this inquiry. As a first approximation we can regard the three-part model as operating thus:

| Individual energy requirements | x | numbers of individuals | x | feeding habits | = | impact as consumers |
|---|---|---|---|---|---|---|

Although this is the general form used in the following studies, we should recognize that the three subroutines of the model, like their counterparts in real life, must be interactive rather than strictly multiplicative (Fig. 2). For example, energy mobilized for production appears in quantum units as "numbers" following reproduction, and failure to obtain required energy leads either to more feeding, or to reduced numbers through departure or mortality. Abiotic variables, primarily temperature, have important effects on each of the subroutines, particularly at or near 0°C.

Figure 1. Trophic relationships of shorebirds, exemplified by calidridine sandpipers, at Barrow, Alaska.

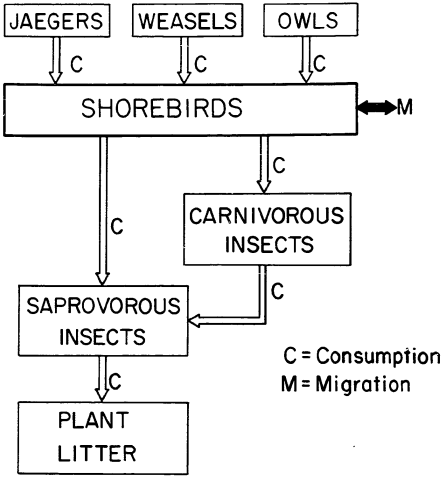
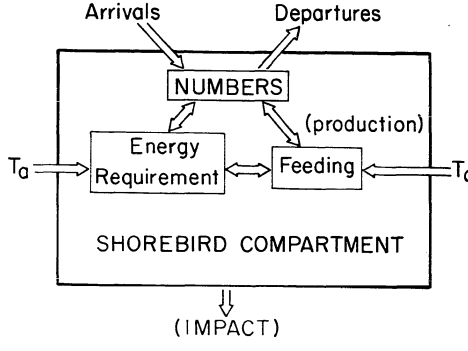


Figure 2. Expanded view of the shorebird compartment, illustrating the interaction of the three components which contribute to the overall impact of the birds on their athropod prey.



The temperature-related progress of snowmelt affects immigration and settling in early summer, ambient temperature affects the availability of energy for production, and temperature affects the rate of emergence, activity, and availability of adult insect prey (MacLean and Pitelka, 1971).

This dissertation is intended to serve as background material primarily for the bioenergetic subroutine of the developing shorebird model, and as an exploration of implications of estimated energy requirements. The studies included here deal respectively with tundra residence and numbers of observed breeding birds (Norton, 1973a), the budgeting of time in incubation during the nesting period (Norton, 1972), the metabolic performance of breeding adults (Norton, 1973b), growth and metabolism of chicks (Norton, 1973c), and the synthesis of this information for estimating total seasonal impact of Calidris species on their resources and evaluating the credibility of these estimates (Norton, 1973d).

The process modeling will be developed in later studies of numbers (Safriel, in prep.), bioenergetics (Norton, in prep.), and distribution of feeding efforts (MacLean, 1972; MS).

# CHAPTER 1.

## PHENOLOGY, BREEDING DENSITIES, NESTING SUCCESS, AND OTHER VITAL STATISTICS FOR FOUR SPECIES OF CALIDRIDINE SANDPIPERS BREEDING AT BARROW, ALASKA

## INTRODUCTION

Analysis of breeding densities, phenology, and annual population variation of the four species of Calidris sandpipers that regularly breed near Barrow is prerequisite to understanding the ecological energetics of each species, and the seasonal impact of the group. Shorebirds, and particularly the calidridine sandpipers, are the major arthropod consumers in the Barrow ecosystem (MacLean and Pitelka, 1971). Norton (1970b) estimated that these four species are collectively the major consumers within the avian community, at least when Brown Lemmings (Lemmus trimucronatus) are not sufficiently abundant to support breeding populations of owls and jaegers.

For convenience, and because the breeding systems of these species need review in terms of estimated resource exploitation, I have followed the terminology of Pitelka et al (MS) in this study, which assesses the relative residence pressure of each species on the breeding ground. The data are presented in schematic form with stress laid upon mean and median values for population parameters to facilitate the estimation of residence (bird-days/ha). This emphasis should not be regarded as typological thinking. The variability of such characteristics as length of chick pre-fledging periods, incubation periods, adult weights, etc., within a species merits thoughtful review elsewhere.

## METHODS

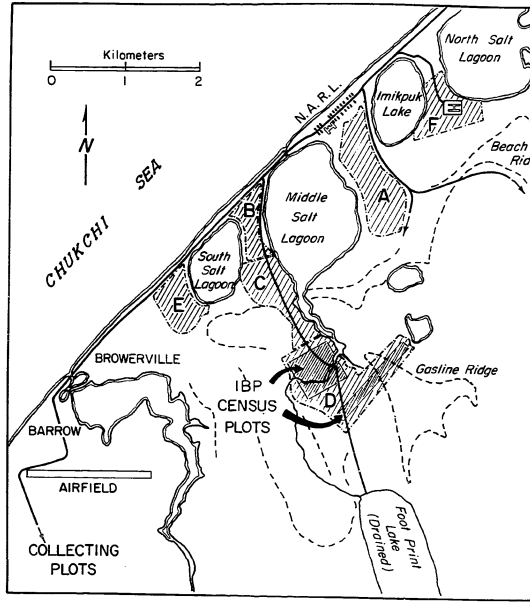
Beginning in 1968 with the Dunlin (C. alpina), records were made of breeding phenology of all birds whose nests could be found in areas

surrounding, and inland of, the Naval Arctic Research Laboratory (NARL) at Barrow, Alaska (Fig. 1). In 1969, Baird's sandpipers (C. bairdii) and Pectoral sandpipers (C. melanotos) were added to the study. The principal innovation over studies of Pitelka (1959), Holmes (1966a-c), and MacLean (1969) was the systematic banding of a proportion of nesting adults and hatchlings so that the fate and movements of individual birds could be followed.

Also in 1968, Safriel (pers. comm. and 1971) began a continuing study of population dynamics in the Semipalmated Sandpiper (C. pusilla). The two of us in combination have therefore covered the four species over the same seasons, and with basically similar methods of observation. All data pertaining to pusilla cited below, were provided by Safriel (pers. comm.) unless otherwise noted.

During the five field seasons 1968-72, 362 nests of alpina, bairdii, and melanotos were followed, and Safriel simultaneously followed about 300 nests of pusilla. We found it convenient to subdivide the Barrow area into six mutually recognized study plots (Fig. 1). The subdivisions were erected arbitrarily, generally bounded by well defined landmarks, convenient to road access, and of manageable size for censusing. Each area was subject to annual changes in size, or even deletion by reason of destruction of the tundra, fencing off, or our inability to census adequately. Figure 1 shows only maximum boundaries for each area: all areas except B and E in some seasons contracted to only half the area shown. (Area G was censused only in 1968, and corresponds to the outline of Gasline Ridge in Fig. 1).

Figure 1. Map of the Barrow area showing the six census areas used 1969-72, with maximum extent of each area shown. (N.A.R.L.: Naval Arctic Research Laboratory).



Nesting densities are calculated only for those areas in which I was confident of having discovered 90-100% of nests present, and which were accessible to observation on a daily basis in a given season. The most rigorous censusing was done on Area D, in conjunction with the Tundra Biome Program of the International Biological Program (IBP). Area D represents the IBP Intensive Site (see Brown 1972:3) and includes within it a bird census plot of 25ha and a transect of 12ha. These two plots were censused at 5-10 day intervals for all species present, and non-breeding as well as breeding birds were counted; thus the ratios of unsettled, or wandering, birds to the breeding population could be estimated.

Censusing of two similar plots at Prudhoe Bay, Alaska (70°15'N; 148°30'W), in 1971 and 1972 by similar methods provided some perspectives on the composition, biomass, and nesting sucess of the Barrow avian community (Norton, et al, in prep.)

Adults were captured for banding and measuring at their nests with a wire mesh drop-trap triggered remotely. Chicks were banded in the nest as soon after hatching as possible. Weighings in the field were accomplished with a series of Pesola spring balances, each nominally precise to 0.5% of scale, but actually somewhat nearer 1-2% of scale owing to windy conditions. Collections of adults and young were generally made off the main study areas, south of Footprint Lake and south of the village of Barrow (Fig. 1). Dead banded chicks were often recovered, however, from small mammal trap lines within the main study areas.

Observations on predation consisted mainly of disappearance of whole or partial clutches before they were due to hatch. In a few instances, the predators -- jaegers (Stercorarius, spp), weasels (Mustela nivalis), Snowy owls (Nyctea scandiaca) -- could be identified by direct observation, or by recovery of bands from casts of avian predators, in the case of predation on chicks. Analysis of predation, not reported in detail here, allowed the establishment of the day of the incubation period by which 50% of all nest predation occurred, predation rates by area and year, and the relationship between waves of predation affecting different areas near Barrow.

For description of the physiography, climate, and biota of the Barrow ecosystem, see MacLean (1969) and Kelley and Weaver (1969).

## RESULTS

The relative timing of breeding events can be compared using clutch completion dates. The dates of clutch completion were observed directly or determined by counting back from the hatching dates using duration of incubation period for each species (Table 1). Figure 2 illustrates the relative promptness of alpina at Barrow, with median clutch completion date preceding that of any other species by a full week. The late spring of 1968, however, severely retarded normal arrival, dispersal, occupation of territories, and nesting for early-breeding alpina, whereas the later-breeding bairdii was not visibly affected (Fig. 2). The relative population synchrony in the onset of breeding was greater in the three monogamous species (excluding probable re-nestings) and least in the

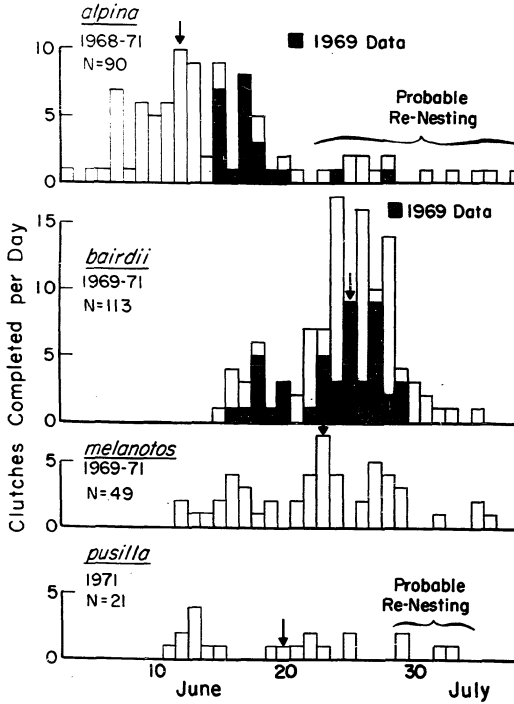
TABLE 1. Incubation periods (from laying of last egg to hatching) of Barrow Calidris species.

| | alpina | bairdii | melanotos | pusilla |
|---|---|---|---|---|
| N | 8 | 16 | 6 | 3 |
| range | 20.5-23.0 | 19.5-21.5 | 19.0-20.0 | 19(2)[2]-21(1) |
| "mean"[1] | 22.0 | 20.5 | 19.5 | 20.0 |

[1] "mean" to nearest half-day.

[2] Data from pusilla nesting at Prudhoe Bay (Norton et al, in prep.).

Figure 2. Clutch completion dates for each of the four Calidris sandpipers at Barrow. Median clutch completion dates are indicated by arrows. The 1969 data for alpina and bairdii are indicated to compare the phenological effect of delayed snowmelt that year on the two species.



promiscuous one, melanotos.

Nesting densities by year and census areas among the species varied annually, as shown in Table 2. C. bairdii reached its highest observed nesting density in 1969 (0.273 nests/ha) while melanotos was the most abundant breeding Calidris species in 1971 (0.205 nests/ha). C. alpina densities were relatively stable, although fewer birds bred near the coast, and on the intensively censused Area D (Fig. 1), in 1972 than in previous years. Most of Safriel's information on pusilla densities was not available for this compilation.

Hatching success was affected primarily by predation, and secondarily by nest abandonment, with a few eggs additionally failing to hatch as a result of infertility or intolerably slow hatching by an embryo (Norton, MS). Egg predation is separated from other causes of nesting failure in Table 3, because it represents a potentially replaceable failure in alpina and pusilla (through re-nesting), and because a large proportion of the remaining nesting failure represented only partial failures within nests, such that the adults did not depart the area but continued to incubate and brood the remaining eggs or young.

The accuracy and completeness of the methods used in this study depended on finding virtually all nests within a census area. Figure 3 shows the relationship of calidridine sandpipers counted during periodic census-taking on the two IBP plots (within Area D, Fig. 1) to the number of birds known to be nesting during the 1971 season. In each species, the number of adult birds unaccounted for by nesting observations dropped virtually to zero, after emigration of pre-breeding flocks, and discovery

TABLE 2. Nesting densities (nests/ha) and hatching success (eggs hatched/eggs laid) by year, area, and species, for Barrow Calidris sandpipers.

| | | Areas: | | | | | | | Barrow [3] | Proportion |
|---|---|---|---|---|---|---|---|---|---|---|
| | Year | A | B | C | D | E | F | G | Ann. Av. | Hatching |
| C. alpina | 1968 | (0)[1] | 0.158 | 0.160 | 0.160 | (0) | (0) | 0.126 | 0.137 | 0.655 |
| | 1969 | (0) | 0.120 | 0.156 | 0.109 | (0) | (0) | ---[2] | 0.101 | 0.970 |
| | 1970 | (0) | 0.160 | 0.178 | 0.171 | 0.050 | (0) | --- | 0.125 | 0.582 |
| | 1971 | (0) | 0.080 | 0.257 | 0.093 | (0) | (0) | --- | 0.118 | 0.725 |
| | 1972 | (0) | 0.040 | 0.200 | 0.078 | (0) | (0) | --- | 0.071 | 0.655 |
| Area Av. | | (0) | 0.116 | 0.190 | 0.122 | (0+) | (0) | 0.126 | | |
| bairdii | 1969 | 0.234 | 0.240 | 0.156 | 0.109 | 0.356 | 0.650 | --- | 0.273 | 0.475 |
| | 1970 | 0.100 | 0.080 | 0.067 | 0.109 | 0.300 | 0.260 | --- | 0.149 | 0.448 |
| | 1971 | 0.333 | 0.040 | 0.057 | 0.139 | --- | 0.080 | --- | 0.147 | 0.278 |
| | 1972 | 0.300 | 0.160 | 0.144 | 0.093 | --- | --- | --- | 0.147 | 0.364 |
| Area Av. | | 0.242 | 0.130 | 0.099 | 0.113 | 0.328 | 0.330 | --- | | |
| melanotos | 1969 | --- | (0) | 0.050 | 0.078 | (0) | --- | --- | 0.019 | 0.800 |
| | 1970 | --- | 0.050 | 0.066 | 0.078 | (0) | --- | --- | 0.046 | 0.685 |
| | 1971 | --- | (0) | 0.299 | 0.357 | (0) | --- | --- | 0.206 | 0.790 |
| | 1972 | --- | (0) | 0.086 | 0.139 | (0) | | | 0.077 | 0.480 |
| Area Av. | | | (0+) | 0.108 | 0.163 | (0) | --- | --- | | |
| pusilla | 1970 | --- | --- | --- | 0.057 | --- | --- | --- | 0.057 | 1.0 |
| | 1971 | --- | --- | --- | 0.139 | --- | --- | --- | 0.139 | 0.455 |
| Area Av. | | --- | --- | --- | 0.098 | --- | --- | --- | --- | |

[1] Indicates area censused, but generally not suitable for that species, and no nests found.

[2] Indicates area not censused for that species.

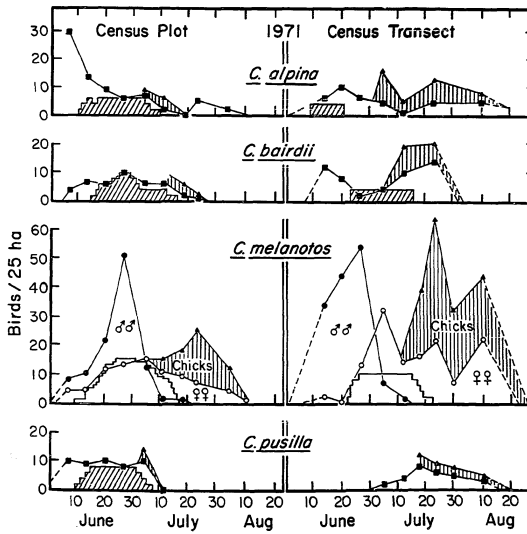
[3] Annual average = nests/total area censused in a given year (not a mean of individual area nesting densities).

TABLE 3. Synopsis of vital statistics, phenology, and breeding systems, for calidridine sandpipers of Barrow, Alaska.

| | alpina | bairdii | melanotos | pusilla |
|---|---|---|---|---|
| Body weights: | 55 60 | 40 45 | 95 65 | 25 30 |
| First arrival | 1 June | 5 June | 5 June | (5 June) |
| Median arrival | 5 June | 15 June | 15 June | (10 June) |
| Median Clutch Completion Date | 12 June | 25 June | 23 June | (20 June) |
| Incubation Period | 22.0 days | 20.5 days | 19.5 days | (20 days) |
| Age of fledging | 20 days | 18 days | 20 days[1] | (18 days) |
| Stage at ♂ Depart | mid-late | fledging* | hatching | fledging |
| Stage at ♀ Depart | August | hatching* | fledging | hatching |
| Territory size | stable | compres-sible | compres-sible | stable |
| Re-nesting | yes | no | (unlikely) | yes |
| Age first breed | 1 yr | 1 yr | unknown | 2-3 yr |
| Nest-site tenacity | yes | no | no | yes |
| Nest predation % (1969-72) | 21.1% | 44.0% | 25.8% | (25%) |
| Median Inc. day of predation | 15th | 11th | 13th | (13th) |
| Overall hatching failure % (eggs failed/eggs laid) | 28.3 | 60.9 | 31.1 | (30) |

* bairdii sex roles may be reversed in some cases -- see text.

Figure 3. Presence of Calidris species compared between census plot and census transect (both within area D) during 1971. Histograms indicate known nesting birds (females in melanotos; both sexes in other spp.). Chick numbers are added to counts of adult birds, but male and female melanotos counts are summed separately.



of nests of resident breeders. The longer a nest was present, the better our chance of discovering it, but the probability of discovery peaked significantly, both immediately after clutch completion, and again just before hatching. The nesting birds not accounted for were mostly those which lost nests to predators in the first 1-2 days after clutch completion. Figure 3 is reassuring, in that it indicates the thoroughness of the method of direct visual censusing and nest search. Figure 3 also provides an impression of relative impact of the species in 1971, a year of extreme melanotos abundance. Areas other than the IBP plot show significantly higher post-nesting incidence of these species when plotted similarly, and hence, a greater presence of young birds through July, as in the IBP transect (Fig. 3).

BANDING RESULTS

The effort to follow individual birds within and between breeding seasons yielded important information and insights into the breeding biology of all four species. Results from banding, including those reported by Safriel (1971 and pers. comm.) are enumerated as follows:

1. Sex roles in incubation have been summarized by Norton (1972). For the purpose of this study, we need only recognize that alpina, bairdii, and pusilla incubation is shared approximately equally between adults, while female melanotos incubate alone.

2. Sex roles in brooding young were determined for alpina and pusilla. The former share brooding duties, while females of the latter were found generally to leave Barrow and the care of young within several

days of hatching (Safriel, 1971). This feature of bairdii's breeding system was studied as rigorously as possible, by observing banded adults, supplemented by collecting and sexing adults with broods. The sexual dimorphism in bill lengths of bairdii is least of the three monogamous species, leading to uncertainties of determining sex by that method (MacLean, 1969). Apparently either sex may remain with the young, although males predominate in brooding. Of 36 broody bairdii collected from 1969 to 1972, 22 were males, and the chicks attended by males were heavier -- mean of 18.7g vs. mean of 13.6g -- and presumed to be older. The visual determinations made on banded pairs with measured bill lengths over the same seasons also favored supposed males in the brooding role, 20 to 7. There was only one possible instance of both sexes sharing in brooding beyond the day of hatching.

3. Re-nesting commonly occurred following nest loss in alpina, and banded pairs were seen to complete a clutch in somewhat under 6 days after losing the first nest. Similarly, pusilla can complete a replacement clutch in 5 days (Safriel, 1971). No banded bairdii or melanotos were seen to re-nest following predation or other nest failure.

4. Movements of breeding adults with respect to nest site and territory defended were relatively unrestricted in all but alpina. Off-duty incubators of bairdii, pusilla, and melanotos could be found at some distance from the nest, sometimes in the company of other conspecific nesting birds, especially in cases of locally high nesting density. The post-hatching movements of attended broods in all species varied. Most alpina and pusilla brood groups moved several hundred meters in the first

few days, then settled in a new area remote from the nesting site for much of the remainder of the pre-fledging period. Both bairdii and melanotos broods tended to move more steadily between hatching and fledging.

5. The approximate ages of fledging were observed among banded young (see Table 3).

6. Mate-faithfulness, philopatry, and nest site-tenacity -- a co-active set of characteristics typifying the conservative approach to breeding -- were determined on the basis of returns of banded birds (see Table 3, 'nest-site tenacity'). The most notable finding of this study is that bairdii at Barrow show none of these characteristics. Virtually the entire breeding population is new to the area each year. Three banded bairdii returned to Barrow, all in 1971 (none in 1970 or 1972). These returns assured us that birds did not annually suffer band loss, and represented a return rate of 0.012 (3/251 potential returns). Two birds were recaptured at nests, one as a first-year breeder. A third was found dead under a wire about 1 km inland from its 1970 nest. In no case was the bird found near its nest, or nest of origin from the previous year, nor with a mate from the previous year. Similarly, melanotos individuals appear to be new to the area each year, as no returns have occurred to date.

7. Age of first breeding (Table 3) is known for all but melanotos. Holmes (1966a) reported a high proportion of first year alpina breeding at Ikroavik Lake, about 8 km inland from my study areas. Such was not the case nearer the coast, where alpina nesting habitats became snow-free

about a week earlier than at Ikroavik. Only two of 228 breeding alpina were known by bands to be one-year birds, although the plumage characteristics (which I did not record) might have indicated a somewhat higher proportion of first-year alpina in the breeding population.

A general synopsis of breeding systems of all four species is presented in Table 3, and is shown schematically with respect to date in Figure 4 (pusilla omitted). The dashed lines in the bairdii schema in Figure 4 show what might be the case if bairdii females laid successive clutches, as do C. temminckii (Hilden, 1965), C. alba (Parmelee, 1970), and Actitis macularia (Oring, 1972; Hays, 1973). This serial polygamy is probably ruled out at Barrow by the forced lateness of the season there, owing to the late arrival, and time usually elapsing between arrival and clutch completion in bairdii. (See Discussion for further consideration of the bairdii breeding system.)

## COMPARATIVE RESIDENCY

The quantification of residency on the tundra by each Calidris species during the breeding season requires the development of appropriate units of measurement and comparison. In terms of numbers, it will be useful to determine residency per nesting effort: adult bird x days/nesting attempt (bd·da/nest). Figures from Table 3 are used to develop the estimates presented in Table 4. The residency of alpina is seen to be 2-3 times that for other species, when all values are corrected for average nesting failures, and for the late summer departures of adult and juvenile alpina. Residency is little affected in alpina by nesting

Figure 4. Schematic representation by date of the relation of differing breeding systems to seasonal residency of three calidridine sandpipers at Barrow, Alaska. C. pusilla, similar to alpina, is omitted. Dashed lines in bairdii schema represent a hypothetical (not observed) capacity of bairdii females to lay a second clutch, and incubate it separately -- see text.

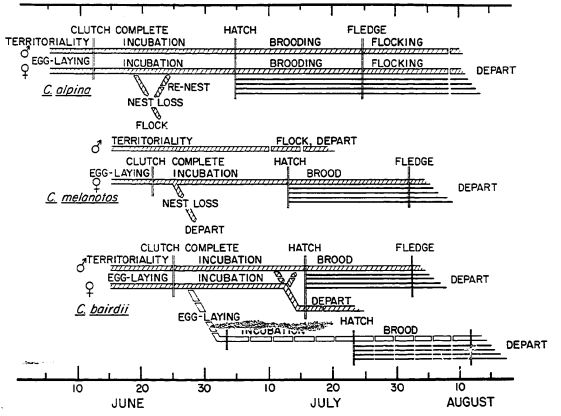


TABLE 4. Estimates of residence per nesting attempt: (adult bird·days/nest) for Calidris species at Barrow, Alaska.

| Species | Figuring | Uncorrected | Corrected |
|---|---|---|---|
| alpina | 2 ad X ($7_{lay}$ + $22_{inc}$ + $20_{prefl}$ + $20_{flock}$) | = 148 ad bd.da/nest | 182.5 ad bd.da/nest[1] |
| bairdii | 2 ad X ($10_{lay}$ + $20.5_{inc}$) + 1 ad ($18_{prefl}$) | = 79 " " " | $61.5^2$ " " |
| pusilla | 2 ad X ($10_{lay}$ + $20_{inc}$ + $2_{brood}$) + 1 ad($15_{prefl}$) | = 79 " " " | $75.5^3$ " " |
| melanotos | 1 ad( ) X ($8_{lay}$ + $19.5_{inc}$ + $20_{prefl}$ + $5_{flock}$)<br>1 ad( ) X (30) | = 82.5 " " | $76.5^4$ " " |

Corrections:

1. alpina a) 50% of 21.1%, or 11% re-nest, since mdn pred. day is 15th of inc period, or 12 June plus 15 = 27 June -- about the last day on which replacement laying should begin annually. Therefore, add: $0.1 \times (2 \text{ ad} \times 15_{inc})$ = 3 ad bd·day/nest. (+)

   b) On the other hand, 10% do not re-nest, so subtract:
   $0.1 \times (2 \text{ ad} \times 7_{inc})$ = 1.5 ad bd·day/nest. (-)

   c) Young remain on the tundra in flocks after fledging for about 25 days, a presence which is essentially like that of adults. Since 71.7% of the eggs laid hatched, and we assume 50% pre-fledging chick mortality, then for every 4 eggs laid, 1.43 will spend 25 days as 'adults' on the tundra, or 35.8 bd·da. (+)

   d) No corrections are made for reduced clutch size of re-nests (Norton, 1972) nor for further predation of re-nests, both of which are considered negligible.

   e) No assessment of adult mortality during the breeding season has been made.

TABLE 4. (Corrections cont'd):

2. bairdii:

a) Since no re-nesting occurs, and adults leave upon nest predation, the reduction in residency will be:

$0.44_{pred} \times 2$ ad $(20.5_{inc\ da} - 11_{mdn\ pred}) = 28.4$ da (-)

and non-re-nesting reduced residencey of the broody adult:

0.44(1 ad) 18 da = 7.94 da (-)

b) Pre-fledging mortality will also cause departures in this species, provided brood size goes to zero. For bairdii, pusilla, and melanotos, the theoretical construct applies, that the probability (P) of total loss of a set of young is related to the probability of mortality of any individual (m) and the number in the brood (n) as follows:

$$P = m^n \text{ (or } \log P = n \log m)$$

Of bairdii nests begun, 44% are destroyed by predators. The remaining 56% are subject further to partial failures, at the level of 17%. Therefore, 39% of eggs laid eventually hatch in 56% of the nests resulting in a brood size at hatching of (39 x 4)/56 = 2.79. The log probability of this average brood size decreasing to zero, assuming a 50% pre-fledging mortality rate is 2.79 log 0.5, or 0.14. If mortality is assumed to be steady over the pre-fledging period, then by the 9th day of chick life, half of potential mortality will have occurred, and therefore:

0.14 x 1 ad x 9 da = 1.26 da (-)

c) Corrections not attempted: nest abandonments, amounting to about 10% of hatching failure, are accounted for only in b), above, albeit imperfectly. Assigning a date for nest desertion is difficult because incubation may cease gradually, or only one adult may persist. Adult mortality is not assessed.

3. pusilla:

a) Re-nesting: by analogous reasoning with the alpina re-nesting correction:

0.06 x 2 ad x 13 da = 1.5 da (+)

0.06 x 2 ad x 7 da = 0.75 da (-)

Non-re-nesting also reduces residency of brooding males:

0.06 x 1 ad x 18 da = 1.08 da (-)

TABLE 4. (Corrections cont'd):

b) Mortality of young, and departure of brood-attending males, by analogy with bairdii:

$$P = m^n$$
$$= 0.5^{3.74}$$
$$= 0.024$$

and, 0.024 x 1 ad x 9 ad = 0.26 da (-)

c) Corrections not attempted: see 1,d,e,2c.

4. melanotos:

a) Nest predation, in the absence of re-nesting, reduces female residency to 50% of the predation rate (0.258) by the 13th day of incubation, or:

0.5 x 0.258 x 1 ad x 6.5 da = 0.8 da (-)

and 0.258 x 1 ad x 20 da = 5.15 da (-)

b) The mortality of young (assumed to be 50% for prefledging period), will cause departures of females by analogy with the bairdii and pusilla situations:

$(0.5^{3.71})$ (1/2 pre-fledging period) (1 ad)

0.025 x 10 da x 1 ad = 0.25 da (-)

c) Corrections not attempted are the same as those omitted for the preceding species.

failure or pre-fledging chick mortality, since adults remain on the tundra regardless of the fate of their breeding efforts. The first flocks of uncommitted birds annually formed near the coast in mid-July. Some of those alpina must have failed at breeding, since it was too early for most to have successfully reared young birds to independence. The residence of bairdii is reduced to 61.5 bd-day/nest from the basic uncorrected value of 79.0, chiefly by the heavy nest predation on that species at Barrow. Individual male melanotos known to breed at Barrow probably did not remain more than 25 days, but the commonly observed influx of flocks of "rogue" males about 25 June (see Fig. 3) led me to estimate an extra 5 bd-da for each nest (Table 4). Despite the ruckus these males created, relatively few of them appeared to succeed in holding territory for any length of time, or in breeding (cf. Pitelka, 1959; MacLean, 1969).

The corrected figures from Table 4 are used to estimate density of calidridine impact in adult bird x days/ha by using the nesting densities given in Table 2. This residency per unit area is presented in Table 5. Each area had a different nest failure rate for each species in a given year, but individual corrections for area and year are not used in the figures in Table 5. The species' average nest predation and hatching failure corrections come closer to predicting the residency observed on formally censused areas (IBP plot and transect in Area D, Fig. 1) than do locally corrected figures. The higher the nesting density and/or hatching success for an area, the more sharply residency was curtailed later in the season, and vice versa. The result is that birds "average" their

TABLE 5. Residency per unit area of four species of Calidris sandpipers at Barrow, Alaska (adult bird·days/ha) by year and area.

| | Year | Area: A | B | C | D | E | F | G | Barrow Ann. Av.[3] |
|---|---|---|---|---|---|---|---|---|---|
| C. alpina | 1968 | (0)[1] | 28.8 | 29.2 | 28.8 | (0) | (0) | 23.0 | 25.0 |
| | 1969 | (0) | 21.9 | 28.5 | 19.9 | (0) | (0) | ---[2] | 18.4 |
| | 1970 | (0) | 29.2 | 32.5 | 31.2 | 9.2 | (0) | --- | 22.8 |
| | 1971 | (0) | 14.6 | 46.9 | 17.0 | (0) | (0) | --- | 21.5 |
| | 1972 | (0) | 7.3 | 36.5 | 14.4 | (0) | (0) | --- | 12.9 |
| Area Av. | | (0) | 21.2 | 34.8 | 22.3 | (0+) | (0) | 23.0 | |
| bairdii | 1969 | 14.4 | 14.8 | 9.6 | 6.7 | 21.9 | 40.0 | --- | 16.8 |
| | 1970 | 6.2 | 4.9 | 4.1 | 6.7 | 18.5 | 16.0 | --- | 9.2 |
| | 1971 | 20.3 | 2[illegible] | 3.5 | 8.5 | --- | 4.9 | --- | 9.0 |
| | 1972 | 18.5 | 9[illegible] | 7.0 | 5.7 | --- | --- | --- | 9.0 |
| Area Av. | | 14.9 | 8.0 | 6.1 | 6.9 | 20.2 | 20.3 | | |
| melanotos | 1969 | (0) | (0) | 3.8 | 6.0 | (0) | (0) | (0) | 1.5 |
| | 1970 | (0) | 3.8 | 5.0 | 6.0 | (0) | (0) | --- | 3.6 |
| | 1971 | (0) | (0) | 17.5 | 27.3 | (0) | (0) | --- | 15.8 |
| | 1972 | (0) | (0) | 6.6 | 10.6 | (0) | (0) | --- | 5.9 |
| Area Av. | | (0) | (0+) | 8.3 | 12.5 | (0) | (0) | --- | |
| pusilla | 1970 | --- | --- | --- | 4.3 | --- | --- | --- | (4.3) |
| | 1971 | --- | --- | --- | 10.5 | --- | --- | --- | (10.5) |
| Area Av. | | | | | 7.4 | | | | |

[1] (0) area censused, no nests found.

[2] (---) area not censused.

[3] Total bird·day/total ha censused in a given year.

residency over available appropriate habitat. Figure 3 illustrates the relative scarcity of Calidris adults with broods from the census plot of Area D in 1971, thus reducing bd·da/ha from the higher level predicted by using local corrections.

As a final operation, adult weights (Table 3) are multiplied by residence per nesting attempt, and compared with the average increment per nest in biomass represented by fledged young, using average nesting success and assumed pre-fledging chick mortality of 50%. No claim is made for bioenergetic relevance of these estimates, given in Table 6, since the biomass is 'packaged' in units of different sizes, each with its own characteristic metabolic requirements. This problem is considered elsewhere (Norton, 1973b). The biomass accumulated per nest in fledged young is related to nesting success and chick survival. The resulting values for bairdii, melanotos, and pusilla "reproductive efficiency" probably do not differ significantly, given the complete uncertainty of pre-fledging chick mortality. C. alpina, however, is only about half as "reproductively efficient" as the other three species, primarily because alpina remain so long, exploiting late summer insect resources (Holmes, 1966a). The productive energy, however, in alpina adults is devoted to a complete postnuptial body molt and fat deposition (Holmes, 1966c; MacLean, 1969; Holmes, 1971) and this later summer residency must be regarded as important in the annual cycle of that species.

## DISCUSSION

The interpretation of breeding systems of calidridine sandpipers as

TABLE 6. Biomass maintained and biomass accumulated per nesting attempt in Calidris sandpipers at Barrow.

| Species | Maintained[1] | | | | Accumulated[2] in fledging young | Reproductive[3] Efficiency |
|---|---|---|---|---|---|---|
| alpina | 5030g·da | + | 5500g·da | = 10,530g·da | 82.3g | 0.08 |
| bairdii | 1405g " | + | 1183g " | = 2,588g " | 33.2 | 0.13 |
| melanotos | 2850g " | + | 3420g " | = 6,270g " | 96.5 | 0.16 |
| pusilla | 1140g " | + | 960g " | = 2,100g " | 38.5 | 0.18 |

[1] using weights of adults from Table 3, and residency per nest attempt from Table 4.

[2] assuming 50% pre-fledging chick mortality throughout, and considering fledged chick biomass as: $\left(\frac{\sigma^{\prime} + \varphi \text{ ad wt}}{2}\right)$ x no. fledged per nest.

[3] reproductive "efficiency": grams accumulated per adult gram x day.

adaptive resource exploitation strategies is valuable in predicting the evolutionary directions of social system development within two broad categories of approach -- the conservative vs. the opportunistic (Pitelka et al, MS). The present study shows, however, that actual resource exploitation may not be discerned solely on the basis of a species' breeding system. If it could be, the three monogamous species would share similar profiles of residence per nesting attempt (Table 4) and of "reproductive efficiency" (Table 6). Tundra resource dependence of the opportunistic, promiscuous species in this study (melanotos) might or might not resemble the other three. In fact, alpina stands out from the other species in every measure of commitment to tundra resources used in this study. Dunlins spend almost 25% of the year on breeding grounds such as Barrow -- far longer than would be required strictly for reproduction -- whereas bairdii, pusilla, and melanotos share a "quick-getaway" strategy towards tundra residency at Barrow. In addition, then, to the series of characters needed to classify a species as to its breeding system, statistics such as those presented in Table 2 and 3 of this study, are required as a first step in assessing the ecological energetics of a population or community of birds.

Strategies for resource exploitation exhibited by these birds should be analyzed with full recognition that the presence or absence of an individual or population is theoretically the outcome of one of three proximate factors: habit, avoidance of an unfavorable situation, or capitalization on a favorable situation. Habit, or more specifically, site-tenacity, and philopatry, are operative in the nesting of alpina

and pusilla (Holmes, 1966a; Safriel, 1971). The opportunism (in the broad sense) of both melanotos (Pitelka, 1959) and bairdii (this study) may be examined for the capitalization or avoidance alternatives. There is, to date, no evidence that the years of melanotos abundance at Barrow have been characterized by especially favorable prey densities (cf. MacLean, 1969; Pitelka et al, MS). As MacLean (1969) demonstrated, the nesting density of melanotos varies directly with numbers and physiological condition of melanotos arriving at Barrow in early June, but this does not rule out the possibility that the birds arrive at Barrow only after sampling and rejecting possible breeding localities to the south. The 1971 winter and spring were cold, late, and snow depths over much of Alaska were above normal. C. melanotos, among other species, may have continued north beyond still snow-covered areas such as the foothills of the Brooks Range, and thus become the most abundant breeding species in that year at Barrow. Other species seen in greater than normal numbers in 1971 were the Whimbrel (Numenius phaeopus hudsonicus) (Cade, pers. comm.; Norton, pers. obs.) and the American Golden plover (Pluvialis dominica dominica), both of which share with melanotos the characteristic of more southerly Alaskan breeding grounds.

The disappearance from Barrow of one adult at about the time of hatching in bairdii, pusilla, and melanotos has been interpreted as having evolved to relieve intra-species competition for insect resources upon which the young birds depend (Pitelka et al, MS). Although the young birds do depend on a temporarily reduced prey biomass (Holmes, 1966b), there is no evidence that available insect biomass could not support

longer residence by the non-brooding adult. Moreover, there is no evidence of reduced nesting density, success, or growth rates among other species in those occasional years when maximum numbers of melanotos adults and chicks compete for the insect prey (Holmes, 1966a; Figs. 1 & 2 and Table 2, this study). The reduction in nesting densities of alpina in 1972 (Table 2) might reflect melanotos-caused inroads on arthropod biomass, but there were relatively few non-nesting alpina seen during the 1972 season, arguing against the notion that a proportion of the population arrived, but were prevented from breeding. No comparable data are available for the last post-melanotos 'high' season of 1964 (cf. MacLean, 1969). At the least, then, we should admit the possibility that the "quick-getaway" strategy represents more properly a case of leaving to capitalize on favorable situations elsewhere, than a case of avoidance of unfavorable feeding conditions at Barrow. Barrow's arthropod resources are sufficiently abundant that post-breeding alpina adults in August are able to utilize the very prey items (Tipula carinifrons larvae, with 4-year life cycles -- or longer -- MacLean, 1971; MS) on which the population depends during the following year (Holmes, 1966b:Fig. 4).

The arrival of bairdii in greater than usual numbers (as in 1969) may reflect avoidance of unfavorable conditions in alpine breeding habitats of the Brooks Range south of Barrow, rather than the capitalization on the Barrow situation. Unlike melanotos, bairdii's breeding distribution is not continuous south of Barrow, but is interrupted in a broad zone from the coast to at least the higher foothills and drier slopes of the Brooks

Range (cf. Irving, 1960), so the two species would not necessarily fluctuate together in abundance at Barrow. The possibility that bairdii might be serially polygamous in the manner of C. temminckii (Hilden, 1965) at Barrow is probably ruled out by the lateness of its arrival and onset of breeding (Fig. 4). Recently, however, MacLean and I examined a male and a female collected on 15 and 21 June 1972, respectively, both showing old brood patches, enlarged (9 x 6 mm) testis in the male, and clear signs of new egg-laying in the female. Both were in heavy body molt normally characteristic of birds finished with nesting in July (MacLean, 1969). While it is possible that both birds had lost nests in the Barrow area and were re-nesting, we have never found re-nesting among banded bairdii, and the dates are too early (Fig. 2) not to warrant skepticism of that theory. Alternate explanations are that these birds either lost nests or deserted a still-incubating partner in some alpine location far to the south of Barrow. The arrival and nesting dates cited for bairdii by Irving (1960) allow this possibility, because up to a full month elapses between the arrival of migrants at Anaktuvuk Pass, and their appearance at Barrow, assuming that this is part of the same mass of migrants. Barrow must, in my opinion, be regarded as a marginal breeding area for bairdii, in view of the heavy predation the species regularly suffers there. The bulk of breeding bairdii at Barrow may be inexperienced first-year birds which 'overshoot' alpine breeding grounds, or, like alpina, get a later start than experienced breeding birds, only to find the more traditional breeding areas fully occupied by the time they arrive. Nevertheless, if even a small fraction of the population nests

in the mountains, then moves to the arctic coast and breeds again, bairdii would represent an important transitional breeding system between monogamy and serial polygamy.

The variability in nesting densities between areas and between years deserves some comment. Areas A, E, and F (Fig. 1) were dominated by nesting bairdii and pusilla. There, dark, sparsely vegetated and xeric high-centered polygons, surrounded by wetter troughs with grass and sedge cover provided favored nesting habitats and nest sites for bairdii and pusilla. Areas B-D had a more complete spectrum of physical relief and vegetative cover types than A, E, and F, and all species were found in those areas nesting regularly. Annual variation in Calidris breeding on areas B-D seemed to be related to the availability of snow-free tundra early in the season. These areas were exposed by the general eastward slope to strong snow erosion by prevailing winter winds, a condition accentuated by dust fallout from the loose gravel originating on the road traversing areas B and C (Fig. 1; Norton, 1970b). The west side of the road characteristically became snow-free from the coast to the IBP sites before tundra inland or to the east, each spring of the study. In years of a late spring (1969, 1971) the early availability of these areas allowed early and denser nesting relative to much of the surrounding area. This factor may explain why median clutch completion dates for alpina reported here are a week earlier than those for the Ikroavik Lake site (Holmes, 1966a). In addition, the low proportion of first-year birds in these areas, as compared to Holmes' (1966a) nesting population, may be attributed to the ability of more experienced, and perhaps already-mated

alpina to occupy exposed ground more quickly as it becomes available.

The increase of dust fallout on area B over the years of this study was associated with increased vehicular traffic, and seemed to decrease the area's attraction of nesting alpina and bairdii. Either the area became snow-free before any birds were ready to occupy it, or the dust and gravel deposited on the tundra surface reduced availability of prey or habitat acceptability in some manner. The far-reaching effects on breeding schedules and overall productivity of such apparently trifling alterations of the physical environment illustrate the delicacy of mechanisms governing the timing and extent of breeding.

The weakest point in this study is our ignorance of chick mortality. Safriel (in prep.) has collected information on this parameter in pusilla. Soikkeli's (1967) study of alpina in Finland showed that 65% of post-hatching mortality was concentrated in the first three days of chick life. Therefore, the assumed median departure date for adults losing broods (footnotes, Table 4) may be incorrect, and probably should be earlier. The measures of adult residency are not very sensitive to changes in assumed chick mortality. Using the data from Table 4 on bairdii for illustration, bird days/nest assuming 25% chick mortality would be 64.0; for 50% -- 61.5, and for 75% -- 59.0 days/nest. The figures in Table 6 are more strongly affected by variation in the assumed chick mortality, and in other studies considering the energetics of populations, the impossibility of determining survival rates of chicks imposes a substantial error on estimates.

CHAPTER 2.

# INCUBATION SCHEDULES OF FOUR SPECIES OF CALIDRIDINE SANDPIPERS AT BARROW, ALASKA

[This section of the dissertation is reprinted from CONDOR 74:164-176. It contains results and conclusions based on three field seasons, 1968-70. Subsequent observations, in 1971 and 1972, have led to changes in several conclusions, which are reported in the Appendix at the end of this section.]

Please Note:

Pages 41-54, "Incubation Schedules of Four Species of Calidridine Sandpipers at Barrow, Alaska, copyrighted reprint from The Condor, not microfilmed at request of author. Available for consultation at University of Alaska Library.

University Microfilms.

APPENDIX -- Addenda and Interpretative Remarks:

1. Subsequent to submission of this study, the incubation period of C. melanotos was determined on the basis of six successful nests discovered before clutch completion in 1971 (Norton, 1973a). The length of this period ranged from 19.0 to 20.0 days, and averaged 19.5 days, making it shorter than any of the other Barrow calidridine sandpipers by a full day (and 3.5 days shorter than I suspected -- Norton, 1972:169). This finding is surprising in view of the relatively large egg size, and the lower proportion of time the eggs are attended.

A seventh melanotos nest, discovered before clutch completion in 1971, was intermittently incubated by the female, which had lost one eye (whether before or during incubation is unknown). That nest hatched on the 30th day after the fourth egg had been laid, and despite the prolonged periods during which the eggs were left at ambient temperatures near freezing, four healthy chicks resulted. They were taken to the laboratory for observation, and all gained weight rapidly for three days before being released to the care of a broody adult female.

The relatively short normal incubation period of melanotos is accompanied by a correspondingly rapid rate of evaporative water loss from the eggs (Norton, 1973b:Fig. 6), and although fresh melanotos eggs are about 1g heavier than alpina eggs, the hatchling weights differ by only 0.4g. It is not clear, however, from MacLean's (1969) data on egg composition whether fresh melanotos eggs have a higher water content than the other species. The rate of evaporative water loss of melanotos eggs (0.15g/egg·day) corresponds to that of a Redshank (Tringa totanus) with a

fresh egg weight 9g greater (22.3g) than that of melanotos (Drent, 1967: Appendix).

2. The hypothesis advanced in this section, relating rapid hatching to adult inattentiveness, was tested in 1971 by repeatedly forcing incubating adult birds off nests showing signs of impending hatching during cold and snowy weather. As predicted, the five nests so treated began to hatch, despite the unfavorable weather. Another three undisturbed nests, judged to be at about the same stage initially, were 18-24 hrs slower in hatching. Although these observations are not proof of the hypothesis, the five nests (3 melanotos, 2 alpina) were the only nests under observation to hatch on that particular day. The probability of selecting by chance the five out of eight nests destined to hatch earliest is low: $(5/8)^5 = 0.095$, or about 1 in 10.

3. Freezing injury is apparently not as important a determinant of incubation schedules as is the urgency of maintaining rapid embryonic development. The threat of frost damage to embryos is apparently minimized by biochemical adaptations resulting in low supercooling points among fresh Calidris eggs, and resistance to chilling injury later in embryonic development (cf. Norton, MS).

# CHAPTER 3.

# RESPIRATORY METABOLISM AND ENERGY BUDGET DURING THE NESTING PERIOD IN CALIDRIDINE SANDPIPERS AT BARROW, ALASKA

## INTRODUCTION

Reproduction in birds involves mobilizing energy for production, and has widely been found to be a metabolically expensive process (Kendeigh, 1949; West, 1960,1968; Drent, 1967; Brenner, 1968). In addition to the energy required for non-breeding birds to maintain constant body weight, and perform the minimum necessary feeding movements, breeding birds generally must invest energy to some extent in egg-production, courtship, incubation, brooding, and caring for young. This study examines metabolic performance of adult sandpipers of the genus Calidris at Barrow, between their arrival there in early June, and the hatching of young in mid-July.

The energy expenditure by these sandpipers during breeding is of especial physiological and ecological interest for the following reasons:

1. Long distance migrations precede and follow the brief tundra residence of each species;

2. Low air temperatures prevail on arctic coastal tundra throughout the brief summer, requiring an apparently high metabolic rate for the maintenance of homeothermy in these small (25-65g) birds;

3. In the absence of song perches, or pronounced topographic relief, most of the courtship and advertisement of territory is performed in flight display (Pitelka et al, MS). Tucker (1968) has shown that such flight requires 8-12 times the resting metabolic rate;

4. All these birds lay four relatively large eggs, representing the production of 80-100% of the adult female's body weight over a four-day interval;

5. The eggs are incubated in shallow, sparsely insulated depressions in the tundra surface during June and early July. This incubation represents extension of homeothermy during a period when mean daily minimum temperatures are near or below 0°C (Brown, 1968).

6. Interspecific overlap among the adults of these species is high, both in food items selected from the tundra arthropod fauna of low diversity (Holmes and Pitelka, 1968), and in feeding style (MacLean, 1969).

In view of their metabolic extravagance suggested by these observations, and the relative abundance of each of these coexisting species (Norton, 1973a), it is not surprising that together, these birds were estimated to be the most important avian consumers at Barrow (Norton, 1970b). By exploring individual energy requirements of adults in detail in this study, we will be in a position to multiply individual requirements by numbers of birds (Norton, 1973a) to estimate the seasonal impact of the population (Norton, 1973d).

## METHODS

Field measurements of oxygen consumption were made at Barrow in three seasons, 1970-72, using a Beckman Fieldlab polarographic macroelectrode in the recirculated atmosphere of a closed system respirometer. A Leeds and Northrup 10mv recorder displayed the output of the oxygen analyzer. The animal chambers were made of clear plexiglass, measuring 12 x 12 x 16.5cm, with a removable top through which intake and exhaust gases were conducted separately, and through which passed thermistor leads to record ambient temperature, wires to electrocardiograph leads, and

wires to small incandescent light bulbs, all in airtight plastic conduit. Electrocardiograms for monitoring heart rate were taken with a Hewlett Packard model 1500a electrocardiograph, connected to right and left patagia (primary leads) and to loose skin of the dorsum (common lead) with small subdermal safety pins. Water vapor was removed from the system with Anhydrone, and $CO_2$ was absorbed with Ascarite. A small freezer with thermostatic control and fan accomodated the animal chamber for low temperature runs, and a heated circulating water bath allowed runs to be made at temperatures above 28°C. Cloacal or esophageal temperatures were measured before and after experiments run below -10°C to check on the ability of observed metabolic rates to counteract heat loss.

Adults were captured at the nest using a wire mesh drop trap triggered remotely, and brought to the laboratory in a darkened cage. Measurements were also made with the chamber darkened, except for about half those made on female melanotos, in which the chamber was illuminated by two 0.04 amp 12-v DC bulbs. The bulbs did not produce a measurable increase in chamber temperature yet were bright enough that observers and subjects could discern features of the chamber interior. Each bird was allowed 20-40 min of equilibration at the experimental temperature with the system open to room air before the first measurement was made. Repeated runs at a single temperature in 1970 led me to select that time span as adequate to minimize the effects of capture and handling before respirometry. Temperaments of individuals varied, and we early discovered that those that would not calm down at room temperatures could be quieted if the first exposure and measurements were made at or below

0°C. The degree of restlessness and muscular activity of a bird in a darkened chamber could be gauged by the activity of the electrocardiograph pen, which was audibly forced off-scale at high gain by gross muscular activity. Any but the briefest struggles terminated attempts to measure oxygen consumption at that temperature until the subject quieted down. Generally, runs were attempted on an individual at two different temperatures selected from between -30 and +35°C, within a single captivity period. Record was made of the order of temperature exposure, since Pohl (1969) found the sequence to produce different estimates of RMR. Experimental runs were usually 10 min or longer, but in no case was the percentage of $O_2$ allowed to drop below 18.5%. Following each determination, the system was opened, and checked for a return to a 20.9% reading of room air oxygen.

The individually color-banded birds were released after experiments, and examination for any injury from EKG leads. Most returned to their nests within 1-2 hr, subsequently to be found incubating normally, although in a few instances, their nests had been taken by predators in the 1-4 hr interval of the respirometry.

Two variants of the above system were used to measure the oxygen consumption of incubating C. bairdii in 1971. (The species and individual pair were chosen for their exceptional tameness.) A clear plastic dome was installed over a bairdii nest convenient to an AC power source, and the outlet gas pumped through plastic tubing to the rest of the oxygen analysis system, plus a flow meter, such that it could be run as an open flow apparatus. Because the nest was only two days from hatching

by the time satisfactory weather conditions prevailed (cloudy skies, temperatures 0-5°C) the embryos were consuming oxygen at a measurable rate, and a clutch of hard-boiled bairdii eggs was repeatedly substituted for the live eggs to get differential oxygen consumption of the adult alone, vs. adult plus embryonic metabolism. On two subsequent nights (22:00 to 01:30) the system was converted to a closed one, and open-flow and closed system measurements made alternately for comparison. The conversion to a closed system necessitated returning gas to the dome through plastic tubing and an inlet port, and sealing the dome to the ground. The sealing of the base of the dome was accomplished by forming a ring of gravel several cm thick under the edge of the dome, laying a sheet of polyethylene plastic over everything except the eggs, and forming a water-filled channel in gravel and plastic sheet into which the dome fitted snugly. Manipulation of the dome and sealing it were done remotely by pulling gradually on monofilament fishing line attached to the dome, and counteracted by rubber bands attached to a stake nearby. Both adults came to tolerate the instrumentation, showing no signs of alarm to the lowering of the dome over the nest, and would incubate quietly for periods at least as long as 90 min.

Determination of the caloric content of eggs was made by vacuum freeze-drying homogenized samples to constant weight, and combustion in a Parr adiabatic oxygen bomb calorimeter. Lipid contents of eggs and hatchlings were estimated by Soxhlet petroleum ether extraction of samples previously homogenized and dried to constant weight. Oxygen consumption by embryos was measured with a manometric system, involving a test flask

with $CO_2$ absorbant (Ascarite) and a compensation flask (Norton, 1970a), which could be submerged in a circulating water bath of controlled temperature. Field weights of adults were measured with a series of Pesola spring balances at the time birds were banded.

## RESULTS AND DISCUSSION

Resting metabolic rates (RMR) in each of the four Calidris species were temperature-dependent, as shown by linear regressions in Figure 1. Thermoregulatory capacities of C. alpina, bairdii, and pusilla were exceeded by chamber temperatures of -24.0, -27.5, and -18°C, respectively (see Fig. 1 -- circled points). Cloacal temperatures following these experiments were below 38°C, the lowest being that of a pusilla recorded as 31.1°C following 45 min at -18°C. Normothermy ranged from 39.5 to 42.9°C in all species when measured at capture. Metabolic inadequacy was also indicated in the cold exposure experiments by a decline in heart rates, which varied directly with RMR in all species, although low correlation coefficients in bairdii and pusilla indicate considerable variability in this relationship (Fig. 2). No failure to maintain normothermy was noted in melanotos females at similar chamber temperatures.

Factors that did, and did not appear related to resting metabolism must be enumerated in order to understand what RMR is measuring, and how it relates to the energetics of the breeding cycle:

1. There was no evidence for a clear zone of thermoneutrality (a range of temperatures over which RMR remained stable and minimal). In the range of ambient temperatures normally encountered in the Barrow

Figure 1. Oxygen consumption (RMR) as a function of temperature in adults of four species of calidridine sandpipers. Overall regression curve for each species is shown as a thick line. Thin-line arrows indicate individuals' performances in successive runs at either higher or lower chamber temperatures. Circled points indicate birds which showed hypothermia, slower heart rates, and reduced oxygen consumption rates. These points were not included in the calculation of the linear regression equations.

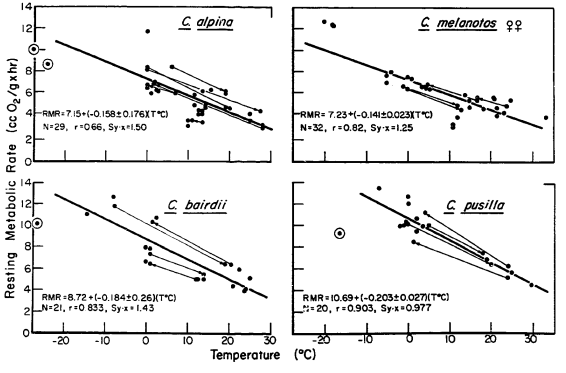
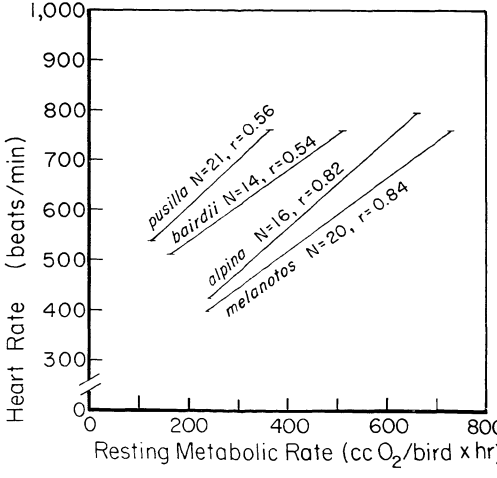


Figure 2. Regression curves of heart rates on resting metabolic rates in adult Calidris sandpipers.



environment (-5 to +15°C) all species appear to be continually expending energy on thermoregulation above the minimum, or standard metabolic rate.

2. The regression curves for the four species generally follow the predicted relationship between body mass, metabolic intensity, and thermostatic heat requirement, in that the largest birds (melanotos females and both sexes of alpina: 55-65g) had the lowest metabolic intensities (i.e. per gram body weight) and least steep regression lines on temperature. C. bairdii adults (35-50g) were intermediate, and pusilla (25-30g) showed the highest metabolic intensities and steepest temperature regression of RMR.

3. Metabolic rates of a bird run at two different temperatures during a single captivity period were almost invariably either higher at both, or lower at both with respect to the species' average. The magnitude of the deviations from average were generally similar at both temperatures, regardless of the sequence of high- and low-temperature exposure (arrows, Fig. 1).

4. A single individual, re-captured at another stage of the incubation period, often differed markedly in metabolic performance from its previous experimental encounter.

5. The highest metabolic rates in each species were those of birds with uncompleted clutches and those captured just prior to, and during hatching.

The pronounced excursions in individual RMR from the species' average could not be reduced by the following manipulations of independent variables:

6. Plotting the RMR as a function of the time of day during measurements produced no discernible pattern, although measurements were made over a 14-hr span, 11:00 to 01:00.

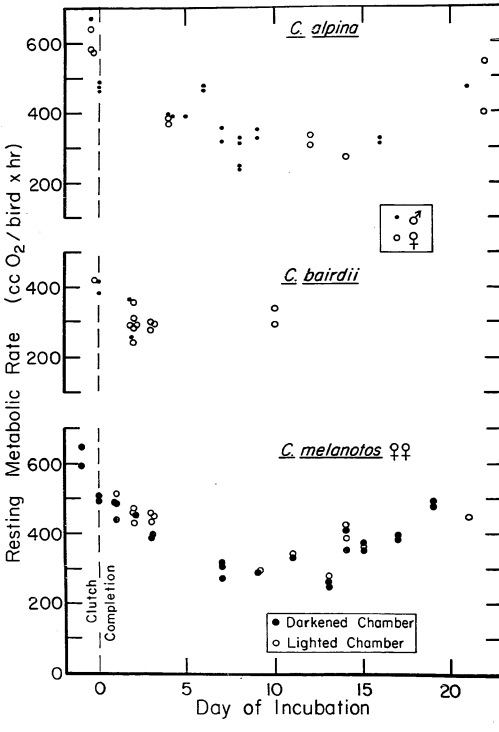
7. No pattern emerged from plotting results as a function of date.

8. Likewise, no reduction in variability of RMR occurred when the approximate environmental temperature at the time of capture (taken from nearest 3-hr interval temperature log, U.S. Weather Station, Barrow) was used as the independent variable.

9. Metabolic rates of female melanotos were only slightly higher in the lighted than in the dark chamber (Fig. 3). Light leaks into the chamber occurred however, even in the 'dark' condition at all temperatures, despite the measure of wrapping a black cloth around the chamber when the laboratory lights had to be on for other reasons during room temperature runs. No conclusion about light sensitivity of adult RMR can be inferred from this operation, which was primarily designed for use in chick respirometry.

The final manipulation was suggested by the high RMR's of birds during laying and hatching periods. Oxygen consumption was plotted as a function of incubation day, with the additional refinement of correcting the RMR to Barrow mean daily temperatures on each day of the incubation period, using the median date of clutch completion for each species (Norton, 1973a) as the starting point. This correction was made according to the slope of the species' regression formula (see point #3, above). No information on the incubation stages of captured pusilla was available at the time of this compilation, and heavy predation on bairdii nests

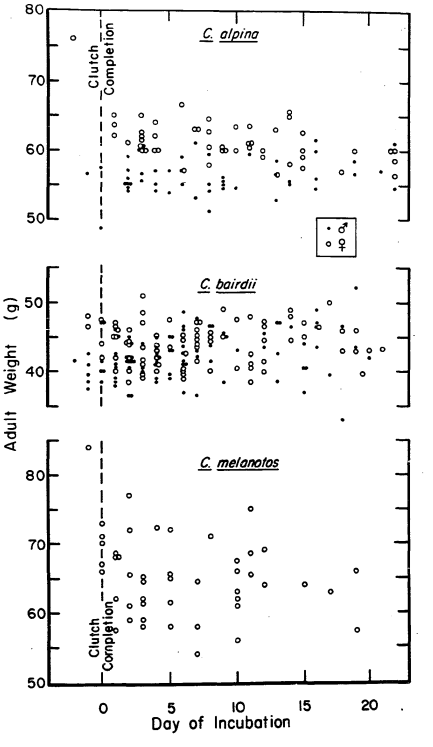
Figure 3. Resting metabolic rates in adult calidridine sandpipers, as a function of incubation stage. RMR's are corrected to ambient temperatures characteristic of Barrow on dates at which 50% of each species population would be at the indicated stage of incubation.



(Norton, 1973a) reduced the usable sample to only six bairdii RMR values that could be assigned to nesting stage. Both alpina adults and melanotos females appeared to consume oxygen at a rate dependent on the stage of incubation (Fig. 3). The expression of RMR values for whole birds, rather than metabolic intensity, gave still less scatter to the points, but raises the question of whether some of the elevated rates might not be the result of greater body weights at laying and hatching. Some of the early higher rates might be the result of residually heavier females at the onset of incubation, but males were generally lighter in both alpina and bairdii at this stage, and the RMR of alpina males was as high as that of females. The weights of all birds banded at the nest between 1969 and 1972, whose nesting stages were determined to $\pm$ 1.5 days, are shown in Figure 4. These show that whole bird RMR did not vary as a function of body weight. The patterns of weight in Figure 4 illustrate species differences in weight variability, and to some degree also the relative importance of fat reserves to the different species (MacLean, 1969, MS): alpina males and females carry the least amount of fat in relation to body weight; bairdii adults are intermediate in fat complement, and weights of the sexes overlap broadly (even granting the fallibility of field sex determination by bill length on live bairdii -- Norton, 1973a); melanotos females have the greatest fat reserves, and the most variable weights during incubation of the three species.

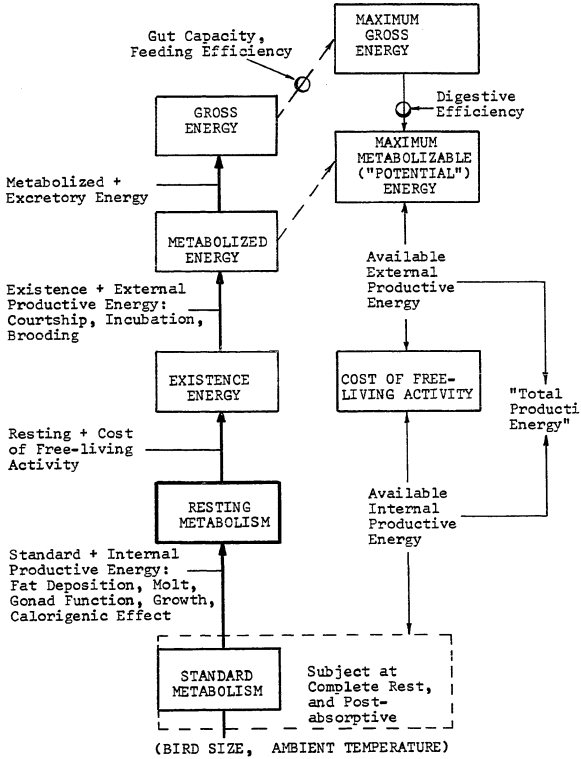
Thus far, the observations suggest that the behavior of the resting metabolic rates during incubation is not spurious: a similar pattern applies for both sexes in alpina, melanotos females, and may be true of

Figure 4. Live body weights of incubating Calidris sandpipers as a function of stage of incubation. Sex determinations on alpina and bairdii were made on the basis of bill length (MacLean, 1969).



bairdii and pusilla. The few data on bairdii RMR are at least not at variance with the other species). The resting metabolic rate, however, remains undefined. Figure 5 presents an hypothesis, and perhaps a generally useful schematic picture of the energy budget for a breeding or otherwise productively engaged bird. The RMR is considered in respect to more rigorously defined conventional terms in the energetic lexicon. Figure 5 assumes that RMR is greater than standard metabolism levels (SMR), by virtue of "internal productive energy", i.e. demands of molt, gonad function, the calorigenic effect of food in the alimentary tract, and fat deposition or growth. The RMR thus can only be meaningful when the SMR is estimated and the internal productive processes identified. Above the RMR, requirements of free-living activity (foraging, locomotion, etc.) constitute an energetic increment leading to free existence energy, here not to be confused with caged existence, or maintenance energy, sensu Kendeigh (1969a), because it is contradictory to discuss maintenance energy in reference to productively active birds. Total metabolized energy is considered to be existence energy plus "external productive energy" demands of incubation, brooding, and courtship activities. The distinction between external and internal productive energy is strictly operational: the former was assumed to be arrested by temporary capture, while the latter was assumed to continue in force during the period of captivity for respirometry. Metabolized energy is related to gross energy (the caloric value of ingested food) by digestive and assimilative efficiency. The righthand side of Figure 5 shows maximum gross and metabolizable energy in relation to SMR. This side of the hypothesis is

Figure 5. Schematic representation of the relation of resting metabolic rates to standard metabolic rate, free existence, metabolized, and gross energy. Right hand side of diagram represents a breeding bird operating at maximum rates of securing and mobilizing energy, to show the theoretical availability and interchangeability of forms of productive energy.



based on the axiom that there is an upper limit to the rate at which a bird can secure and mobilize energy. In this construct, two predictions can be made. First, as SMR is driven upward by lower temperatures, the total energy available for production is reduced (cf. West, 1960; Kleiber, 1961; Kendeigh, 1969b). Second, reduction of demand for one type of productive energy should result in greater availability of the other type.

We are now in a position to examine estimates of productive energy requirements, to see whether they fit with the predictions of Figure 5, and to build an estimate of at least part of the fate of metabolized energy in sandpipers during the nesting period.

The requirements for egg-production, here defined as internal productive energy, are estimated in Table 1, based on caloric density of fresh egg contents, weights of egg contents, and Brody's (1945) estimate of 77% net efficiency of egg production.

The energy budget for incubation (external productive energy) may be estimated by the formula of Kendeigh (1963), proven applicable to a wide size range of birds (El-Wailly, 1966; Drent, 1967). The parameters used in this slightly modified formula for Table 2 are:

n = number of eggs in the clutch (4 throughout)

w = mean weight of each egg (see Fig. 6)

h = specific heat (estimated at 0.8 throughout)

b = cooling constant (measured -- Norton, 1970a, or estimated according to the observation that cooling constants are proportional to $(\text{weight})^{-1/3}$ for similar-shaped objects -- Kleiber, 1961)

TABLE 1. Estimated energy cost of egg-production in *Calidris* species.

| Species | Egg caloric density (N) | egg dry wt[1] | energy/egg[2] | energy/clutch |
|---|---|---|---|---|
| *alpina* | 7.3 kcal/g (4) | 2.6 g | 24.6 kcal | 98.4 kcal |
| *bairdii* | 7.6 " (2) | 2.1 g | 20.8 " | 83.2 " |
| *pusilla* | [7.4] " | 1.5 g | 14.4 " | 57.6 " |
| *melanotos* | [7.5] " | 2.9 g | 28.2 " | 113 " |

[1] egg contents without shell -- MacLean, 1969.

[2] estimated metabolizable energy requirement, assuming net efficiency of egg-production:

$$\left(\frac{\text{calories of egg produced}}{\text{calories metabolizable energy above maintenance}}\right) = 77\% \text{ (Brody, 1945).}$$

TABLE 2. Daily energy requirement of incubation in Calidris species, estimated by the formula of Kendeigh (1963).

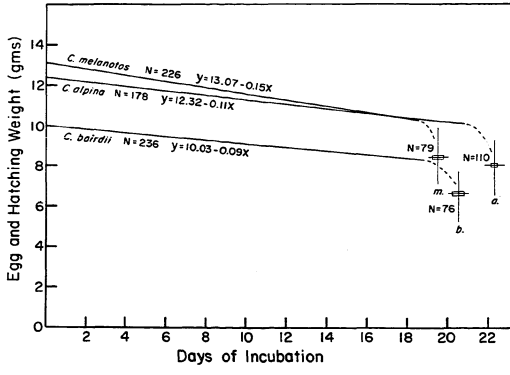
| Species | n[1] | w | h | b | $(T_e-T_{na})$ | i | $(1-c\cdot a)\cdot P^2$ | Kcal/da |
|---|---|---|---|---|---|---|---|---|
| alpina | ♂ 4 | 11 | [0.8][3] | 2.6 | (38.1-25) | 24 | (1-[.25]..98)[0.5] | = 10.9 |
| | ♀ | | | | (13.1) | | (0.755) [0.5] | = 10.9 |
| bairdii | ♂ 4 | 9.0 | [0.8] | 2.9 | ([13.1]) | 24 | (1-[.25]..95)[0.5] | = 10.0 |
| | ♀ | | | | | | (0.762) [0.5] | = 10.0 |
| pusilla | ♂ 4 | [6.2] | [0.8] | [3.14] | ([13.1]) | 24 | (1-[.25]·[.97])[0.5] | = 7.4 |
| | ♀ | | | | | | (0.758) [0.5] | = 7.4 |
| melanotos | ♀ 4 | 11.8 | [0.8] | 2.5 | ([13.1]) | 24 | (1-[.25]..85) 1.0 | = 23.8 |

[1] for definition of symbols, see text.

[2] P - parental share in incubation.

[3] [] - values not measured, but estimated on the basis of other species.

Figure 6. Changes in egg weights over the incubation period in alpina, bairdii, and melanotos. Hatchling weights are shown with mean, range, and standard error of the mean.



$(t_e - t_{na})$ = egg temperature minus nest air temperature (38.1 minus 25.0 -- on the basis of Norton, 1970a)

c = proportion of egg surface covered (assumed to be 0.25 in all)

a = the proportion of time the eggs are incubated (see Norton, 1972)

p = the parental share in incubation (0.5 per adult, except 1.0 in melanotos females)

Evaporative water loss of eggs during incubation amounts to a small, but measurable, increment in the energy requirement for incubation. Weight loss by eggs is nearly entirely due to water loss (Drent, 1967), and hence the weight changes in eggs (Fig. 6) allow us to quantify the energy increment, which is not accounted for by Kendeigh's (1963) formula for the cost of incubation.

At the same time, embryonic metabolism should reduce the required heat input from adults, becoming measurable at about completion of the first third of the incubation period (Drent, 1967). The magnitude of the embryonic contribution can be estimated from the depletion of extractable fat between fresh egg and hatching stages (Table 3). These values give only an approximate estimate of fat depleted, because some of the chicks used for extraction died several hours after hatching, and also, a large fraction of the total depletion may have occurred during the struggle of hatching. Preferably, values should be taken for embryos just before the onset of hatching, to get a more accurate picture of the contribution to incubation energy requirements. The substrate for embryonic metabolism is known to be almost entirely fat (Romijn and Lockhorst, 1956), and the proportion of fresh egg fat remaining at hatching (Table 3) is

TABLE 3. Estimated energy expended by *Calidris* embryos during incubation.

| Species | g fat/fresh egg[1] | g fat/hatchling (N) | fat used | energy/egg |
|---|---|---|---|---|
| *alpina* | 1.06 | 0.44g (6) | 0.62g | 5.9 kcal |
| *bairdii* | 0.97 | 0.36 (4) | 0.61 | 5.8 |
| *melanotos* | 1.09 | 0.51 (2) | 0.51 | 5.1 |

[1] MacLean's (1969) values.

typical of nidifugous birds (Drent, 1967).

The respiratory exchange of full-term embryos (last 24 hr before hatching) was measured on 17 alpina eggs (Norton, 1972a) and 7 bairdii eggs. This measurement (Table 4) provides a second estimate of metabolic activity in embryos at a point in time when they are contributing maximally to the heat balance of the nest, because incubation rhythms have not yet deteriorated (Norton, 1972) and the extreme metabolic output of hatching has also not begun. The metabolic intensity at 38°C was about 2.25cc $O_2$/g·hr in both species, and can be converted to caloric equivalent by 4.7 kcal/liter $O_2$ on the assumption that fat is the substrate (Kleiber, 1961). Full-term embryos are estimated then to contribute 35-40% of the required nest heat balance on the final day before hatching in each species.

Table 5 combines the values from incubation energy estimates (Table 2), the caloric equivalent for evaporative egg water loss (Fig. 6 and 580 cal/g -- Drent, 1967), the embryonic fat energy expended (Table 3), and the incubation periods of each Calidris species (Norton, 1973a), to estimate the embryonic contribution to the overall incubation energy requirements. These range from 4.4% (melanotos) to 5.6% (bairdii).

The final estimate of incubation energy budgeting was attempted by the respirometry on a naturally-incubating pair of bairdii with a chamber at the nest (Fig. 7; Table 6). These measurements should add up to adult RMR plus incubation energy plus embryonic contribution, during the last three days of the incubation period. Ambient temperatures under the plastic dome were consistently 5° higher than environmental

TABLE 4. Laboratory measurements, and estimates of oxygen consumption of full term embryos at 38°C.

| Species | embryo wt | $O_2$ consumption/egg[1] | heat/clutch·day[2] | % of required |
|---|---|---|---|---|
| alpina | 8.0g | 18.0 cc/hr | 8.15 kcal | 37.5 |
| bairdii | 7.6 | 17.1 | 7.7 | 38.2 |
| melanotos | 8.4 | [19.0][3] | 8.2 | 34.5 |
| pusilla | [5.8] | [13.1] | [5.9] | [40.0] |

[1] Data from Norton (1970a).

[2] Estimated on basis of fat substrate - 4.7 kcal/l $O_2$ consumed (Kleiber, 1961).

[3] [] bracketed values are estimates, based on 2.25 cc $O_2$/g·hr for full term embryo, recorded for both alpina and bairdii at 38°C.

TABLE 5. Total incubation energy cost and embryonic contribution in *Calidris* species.

| Species | kcal/ day·nest | Evap. heat loss/day | Days | required Total | embryonic heat produced | embryo share |
|---|---|---|---|---|---|---|
| *alpina* | 21.8 | 0.265 kcal | 22.0 | 436 kcal | 23.6 kcal | 5.4% |
| *bairdii* | 20.0 | 0.21 | 20.5 | 414 | 23.2 | 5.6 |
| *melanotos* | 23.8 | 0.35 | 19.5 | 472 | 20.2 | 4.4 |
| *pusilla* | [14.8] | [0.16] | [20.0] | [300] | 16.2 | 5.4 |

Figure 7. Open-flow system for determining oxygen consumption by a naturally incubating adult at a bairdii nest. The plastic lid was drawn over the nest when an adult was present, and oxygen content of the air drawn through the system was determined. Subsequently, this system was converted to a closed flow configuration by returning air through a second plastic tube -- see text for details.

TABLE 6. Field measurements of adult and egg respiration of C. bairdii summarized.

| Incubation Day | Open Flow System | | Closed System | |
|---|---|---|---|---|
| | ad, live eggs | ad, dead eggs | ad, dead eggs | live eggs |
| 19th | 306cc $O_2$/hr | 252cc $O_2$/hr | - | - |
| 20th | - | 277 | 290cc $O_2$/hr | - |
| 21st | 419 | - | 310 | 96 |

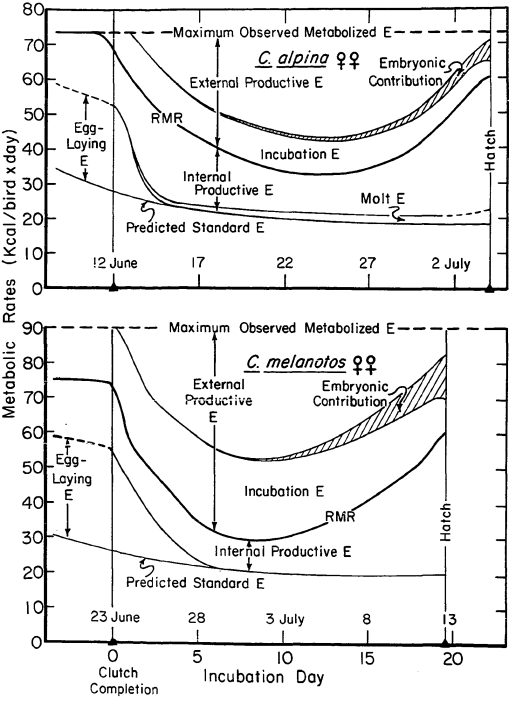
temperatures, and varied only between 6 and 10°C, such that temperatures were not a factor in interpreting the observed metabolic rates. The oxygen consumption of the four live eggs may be represented by the difference in oxygen consumption observed between adults' sitting on live eggs over that of sitting on dead eggs. If so, the clutch respiration rate rose from 54cc $O_2$/hr to 96cc $O_2$/hr between the 19th and 21st day of incubation. These values are somewhat higher than predicted by laboratory egg respirometry (Table 4). On the other hand, one could argue that the embryonic metabolism should be compensatory and that the total metabolic rates, whether with adults on live eggs or dead eggs should be the same, leaving us to conclude that variability accounts for the different readings under the two conditions. Adult RMR should have been about 280cc $O_2$/bird·hr, or higher if a late-incubation peak were detectable in bairdii, plus the cost of heating the eggs, or about an extra 150cc $O_2$/hr (Tables 2 and 4). In view of the measured rates (250-419cc $O_2$/hr) which are lower than expected, one either has to question whether incubation cost is additive to RMR, or to regard the experimental results with suspicion. Because it was impossible to check the system for leaks while operating it as a closed system, or for backflow during open flow operation, I choose the latter alternative. A small leak in closed system operation can result in underestimates of oxygen consumption by 25% or more. The oxygen consumption rates did show one predictable feature during these experiments, however. After the arrival of an adult at the nest, and its sitting on cool eggs, the metabolic rates recorded in either open or closed system were temporarily very high (480-650cc $O_2$/hr)

returning gradually to lower values over a period of time that may have reflected how far below incubation temperature the eggs had cooled in the absence of an adult. (The values quoted in Table 6 are all from steady incubation).

The data and interpretation of resting metabolic rates presented above allow us to consider a partial energy budget for the incubation period of Calidris sandpipers at Barrow. Female alpina and female melanotos offer the best bases for comparison because of the completeness of data and the contrast in their incubation systems. Standard metabolic rates in Figure 8 were computed from the predictions of Kendeigh (1969), using weights of 60.0 and 65.0g for alpina and melanotos, respectively. The SMR was temperature-corrected to the Barrow mean daily temperatures for the dates indicated, which correspond to 50th percentile dates for clutch completion in the populations of each species (Norton, 1973a). RMR values are taken from Figure 1 and converted to caloric values under the assumption of a largely protein diet, hence caloric equivalence of 4.6 kcal/liter $O_2$ consumed (Kleiber, 1961). Incubation requirements are based on Table 2, with the approximate embryonic heat evolution indicated from Tables 3 and 4. Estimated daily egg-production energy, from Table 1, is shown as part of the RMR for each species, and shown to decline over a several-day period following clutch completion. This feature corresponds both to the decline in measured RMR and the finding that the cost of egg-production is spread over a longer period than the interval required to complete the clutch (El-Wailly, 1966).

Molt of primary feathers occurs in both sexes of alpina, beginning

Figure 8. Comparison between estimated partial energy budgets of idealized female Calidris sandpipers representing two-sex incubation (alpina) and single-sex incubation (melanotos).



within several days of clutch completion and continuing throughout the incubation period (Holmes, 1966c). Since ecdysis does not involve insulative feathers and is relatively protracted, it seems adequately generous to assign an energetic increment of 10% over the SMR, or about 2 kcal/bird·day as part of the RMR (cf. King and Farner, 1961; Blackmore, 1969). No molt occurs in incubating melanotos. Body molt in alpina follows hatching (Holmes, 1966c) which might help explain the unresolved question of the increase of RMR late in the alpina incubation period, but body molt in female melanotos is delayed until the chicks are independent (Pitelka, 1959; MacLean, 1969), and the melanotos RMR also shows the increase late in incubation.

If the highest RMR observed in the laboratory represents long-term maximum metabolizable energy, then incubation by melanotos females requires 40% at a minimum, and 100% at a maximum, of the apparent daily external productive energy. The corresponding values for alpina appear to be between 26 and 100% of external productive energy. Estimates of the proportion of energy devoted to incubation in different species have been expressed on different bases -- 28% of existence energy in Spizella arborea (West, 1960); 17-100% of productive energy in Troglodytes aedon (Kendeigh, 1963); up to 18% of productive energy in Taeniopygia castanotis (El-Wailly, 1966); and 20-33% of net energy in Larus argentatus (Drent, 1967). Drent (MS) recalculated these values in terms of available productive energy, and found that each incubating adult in the four species he considered devoted between 16 and 25% of its total available productive energy to incubation.

Drent (1967) further proposed that 25% was the upper limit for this proportion. Each adult of alpina expends in incubation about 20% of total productive energy (metabolized energy minus SMR), but female melanotos require 34% of total productive energy for incubation. The reliance of melanotos females on fat reserves (MacLean, 1969) giving rise in part to the variable weights of incubating birds (Fig. 4), and the 11% shorter incubation period in this species (Norton, 1973a) may minimize the energetic taxation by incubation requirements. Norton (1972) found that the time available for foraging by melanotos females during incubation was 15%, or 3.6 hr daily, as opposed to 12 hr or more in the two-sex incubators. Energetic inadequacy of melanotos incubation strategy has not been shown even in seasons of distinct climatic adversity at Barrow, such as 1963, although MacLean (1969) reported lower body weights of nesting females in that season.

It is difficult to explain elevated RMR in late incubation for either sex, except by attributing it to alertness. Alertness in brooding the young, and more importantly, the "marshalling" of chick movements to prevent predation by jaegers and owls, may require considerable psychic effort which is amplified, in effect, by increased muscle tone or other energy-demanding correlates. If the development of alertness is an explanation for rising late-incubation RMR, then the subtleties of embryo-to-adult communication deserve further investigation. Earlier (Norton 1972: 174) I concluded that behavior changes in calidridine incubation were initiated by changes in the eggs and embryos; that is, adults showed no evidence of a sense of when their eggs should hatch in the absence of

viable embryos.

High early-incubation RMR's of males may also reflect alertness energy, because males are committed to intraspecific territorial interactions, primarily early in the nesting cycle. Additionally, high RMR's at this time may represent the recovery cost from long bouts of aerial displays by males, analogous to recovery from egg-laying in females. Another source of requirement for male alertness is the necessity for establishing a workable incubation routine, possibly involving signalling between the sexes to provide for alternation of sitting spells. I have found each nest to be incubated according to a different schedule of alternation in both alpina and bairdii during the 48-hr incubation checks on banded pairs at 2-hr intervals, and Safriel (pers. comm.) has found the same to be true of pusilla.

Although we do not know that energy is the controlling proximate factor in the apparent biological choices among such alternative processes as molting and incubation, it is worthwhile to hypothesize that this is the case, and review the evidence. In theory, energy might be an extrinsic limiting factor, as when food is scarce. The clutch size in Snowy owls, for example, is related to abundance of lemmings during a particular breeding season (Pitelka et al, 1955). Shorebirds ordinarily do not show any such convenient variability. On the other hand, energy may also be limiting through the intrinsic ceiling of maximum metabolic rate, as proposed by Kendeigh (1949), West (1960) and Kontogiannis (1968). The intrinsic rate ceiling is provisionally adopted in this study (Fig. 5) The estimated total metabolic requirements by both alpina and melanotos

females at the beginning of the incubation period are approximately equal to their respective maximum observed RMR. If this represents a true rate ceiling, it may explain other observations. For example, the virtual absence of incubation by alpina until the third egg is laid (Norton, 1972:Fig. 1) may be explained by intrinsic energy limitiation, as Kendeigh (1963) has interpreted a similar situation in the House wren (Troglodytes aedon). Female melanotos in this study appeared to have a substantially higher maximum RMR than other species: I could not overtax the thermogenic capacities of any of the three females tested at -20 to -34°C. A higher metabolic rate ceiling for melanotos could be adaptive in view of the reliance of that species on single-sex incubation in the arctic.

At the outset of this study, I considered it possible that adaptive reductions in expected energy requirements would be found in these species, in view of their probable long association with arctic environments. They may still individually require less energy than estimated, but the mechanisms for energy conservation are not more than hypothetical. The thermogenic heat requirement may be less than estimated, owing to the calorigenesis of food (S.D.A.) as Kleiber and Dougherty (1934) found in protein-fed domestic chicks. Although the temperature gradient in the "canopy" of arctic tundra affords almost no thermal advantage (Weller and Benson, 1971) over standard weather bureau air temperatures, radiant energy may be advantageously absorbed in plumage. Heppner (1970) found that dark plumage absorbed enough energy significantly to reduce thermal gradients between core and ambient, and thereby reduce the metabolic rate.

The concept of an energy budget studied through the resting metabolic rates of productively active birds, presented as a working hypothesis in Figure 5, was used to predict that a release from one type of productive energy requirement would allow adults to engage another productive process. That prediction is borne out in the breeding systems of Calidris species confronted with egg predation. Cessation of incubation energy requirements in alpina and pusilla commonly results in the prompt initiation of egg-laying for attempted renesting. By contrast, nest loss in bairdii allows both adults to divert productive energy to extensive body molt, premigratory fat deposition, and departure. These are examples of diversion of energy from the operationally defined "external" to "internal" forms, but the converse also regularly occurs as the demands of egg-laying cease and incubation constancy increases dramatically (cf. Kendeigh, 1963; Norton, 1972a:Fig.1).

Further investigation of the compensatory or additive nature of incubation energy with respect to resting metabolism is indicated by the uncertainty surrounding the experiment with naturally incubating bairdii. That experiment also raised the same question about the assumption that embryonic heat evolution is compensatory by reducing the energy cost to incubating adults.

In spite of these possible mechanisms for reduction of individual energy requirements, we must be properly impressed by the apparent volume of energy required by arctic breeding. Continuous daylight at Barrow presumably allows prolonged foraging on prey resources, as well as favoring species which can capitalize on available energy virtually without

interruption during good weather. Another aspect of the Barrow climate to consider is its buffering by marine influence. A species capable of long-term existence near 0°C is in a favorable position to use Barrow for breeding, because pronounced temperature excursions in either direction from between 0 and 5°C are relatively uncommon on such coastal tundra. In this regard, it is perhaps significant that the most persistent resident of Barrow tundra, C. alpina, is the species and population of the four which winters farthest north in the nothern hemisphere. The remaining three species winter in equatorial (pusilla) or southern hemisphere areas (bairdii and melanotos)

The seasonal energetic impact of the breeding activities for these species is considered in a separate study (Norton, 1973d) which includes consideration of the chick growth periods (Norton, 1973c) and the tundra residency and numbers of all birds (Norton, 1973a).

# CHAPTER 4.

# BIOENERGETICS, THERMOREGULATION, AND GROWTH OF CALIDRIDINE SANDPIPER CHICKS AT BARROW, ALASKA

## INTRODUCTION

An investigation of chick growth in a natural avian population to estimate the relative energy demands of growing young necessarily involves two lines of inquiry. The first is the physiological, or autecological, requirement of a growing neonate. The second is that of assessing the chicks as consumers by determining how many survive at a given stage, what food items they require, and what demands they place on the adults of the species. The present study is largely devoted to the first line of inquiry, leaving the second to further refinement of estimates of chick mortality, prey selection (Holmes, 1966b; Holmes and Pitelka, 1968) and social interactions of young and adult birds.

Understanding chick growth processes is important because the population energetics of shorebird reproduction on arctic coastal tundra can be compared to a high risk financial investment, in which the payoff mainly corresponds to the pre-fledging survival and growth of chicks. Even at more moderate latitudes, heavy sandpiper chick mortality occurs during the first 72 hr following hatching (Soikkeli, 1967). At Barrow, the low temperatures and vagaries of weather appear to accentuate the risk of reproductive failure. Ambient temperatures are about 5°C at the peak of hatching, representing a 35° gradient between expected core temperatures of 6-10g neonates (Fig. 1) and the environment. Periods of freezing weather can occur just when the maximum number of chicks are dependent upon surface-active athropod prey (MacLean and Pitelka, 1971). Low temperatures force the chicks to seek adult brooding for warmth, and appear to reduce severely prey availability. By contrast to this situation, largely vegetarian

Figure 1. One-day old C. bairdii chick, approximately natural size (7.5 g), photographed in outdoor pen.

ptarmigan (Lagopus, spp.) chicks use food that is not affected in availability by temperature (Theberg and West, MS).

In certain years, Brown lemmings (Lemmus trimucronatus) attract an array of predators to the Barrow area -- jaegers (Stercorarius, spp.), weasels (Mustela nivalis), Glaucous gulls (Larus hyperboreus), and Snowy owls (Nyctea scandiaca) -- all of which prey facultatively on shorebird chicks. Probability of chick predation may not be independent of adverse weather, which tends to reduce dispersal and mobility of the young, and make them easier targets for predators.

The domination of the Barrow avifauna by breeding shorebirds (7 of 11 terrestrial species) suggests that the high risk investment regularly does pay reproductive dividends. Returns of breeding birds banded in earlier seasons as hatchlings (Safriel, 1971; Norton, 1973a) confirm that suggestion.

Holmes (1966a,b) in his studies of Calidris sandpipers at Barrow was duly impressed by how critical the chick growth period was to the reproductive cycle, and emphasized two observations. First, the timing of breeding tends to place the peak of hatching at the average point of peak emergence of suitable adult insects. Second, the insect prey biomass during adult emergence is the lowest of the breeding season. The simultaneous dependence of adult and young sandpipers of all four Calidris species on this restricted resource base raised the question of intraspecific competition for prey, and has been used to explain the departure of one adult per breeding pair at the time of hatching, in three of the four Calidris species (Pitelka et al, MS).

The present paper is one of a series designed to provide background values and to identify the determining variables in developing a three-part simulation model of shorebird impact on resources. In this series, energetics are considered by Norton (1973b; this study; 1973d); numbers, populations, and phenology of the various species are described by Norton (1973a) and Safriel (in prep); and the feeding subroutine is being developed by MacLean (1972; MS).

## METHODS

Captive rearing of alpina and bairdii chicks was approached as an alternative and supplement to studying growth in the mobile and cryptic wild young (cf. Holmes, 1966a). The three species used here differ in growth rates, age and size attained at fledging, and relative abundance and availability for study (Norton, 1973a). Otherwise, the processes of ontogeny of thermoregulation, brooding requirements, fat deposition, and diet selection were found or assumed to be so nearly identical in each that certain data are lumped without regard to species distinctions and elsewhere data gathered on one species must be assumed to be applicable to the others.

Surveillance of nesting activities, and prediction of hatching dates allowed hatchlings of all species between 1968 and 1972 to be banded at nests as soon as they were dry. Some were taken immediately to the Naval Arctic Research Laboratory for rearing in captivity. All captive alpina and bairdii chicks were reared on an ad libitum diet of Tenebrio larvae, ground beef, and rolled oats, supplemented by ground eggshells and vitamin

A oil, as described by Serventy et al (1962). Sand and water were always available.

Birds were maintained under three different conditions: 1) Indoor captives (N=52) were kept 1-2 per cage in 15 x 45cm "mailbox" cages, consisting of a wooden floor and an arched roof of hardware cloth. A bank of incandescent lights was suspended over these cages for a source of constant heat and light, and temperatures in the cages varied between 25 and 35°C. Food ingestion was measured by item and weight, and excreta was collected at 24-hr intervals for subsequent oven-drying and bomb calorimetry. 2) Outdoor individual captives were reared in 1969 (N=11) in the same cages as the indoor birds, in an unheated Quonset hut, such that the temperatures were maintained 0-20°C above Barrow ambient levels in different parts of each cage. Chicks were put outdoors at the age of 2 or 3 days. Amounts of ingested food and excreta were not recorded. 3) Outdoor communal rearing was attempted in 1970 and 1971 on a total of 32 chicks, which were kept in a 1 x 3m wooden-floored walk-in cage, in which a commercial chick brooder afforded an area of refuge from outside temperatures and wind. Many of the chicks died as a result of a midnight power failure in 1970, reducing the sample size to 14 young overall. The same food as in the other conditions was offered in a shallow tray outside the brooder.

Captive birds were weighed and measured at 1-4 day intervals. Chicks that were either sacrificed, or succumbed to other causes, were used for carcass analysis. Determinations of caloric density (kcal/g) were made on a Parr adiabatic oxygen bomb calorimeter. Lipid contents

were determined by Soxhlet petroleum ether extraction.

Respirometry experiments at different temperatures were made in a closed-system apparatus, with a polarographic oxygen analyzer (Beckman model 777 or Beckman Fieldlab) used to measure per cent oxygen in the recirculated atmosphere. A thermostatically controlled circulating water bath, and a small freezer were used to control temperature of the animal chambers (see Norton, 1973b, for full description).

Metabolic measurements were made only on indoor captive alpina in 1968, using a metal can as the animal chamber, which did not admit light, and many subjects fell asleep during a run. Chick respirometry was not repeated until 1972, when a larger series of wild bairdii chicks of known age was made available by another experiment. Whole broods were caught following collection of the attending adult. In the absence of the adult, chicks could be located by their distress notes and movements. Respirometry using a transparent chamber with remotely controlled lights, allowed the chamber to be illuminated and the observer to check on the activity and wakefulness of the subject. Deep esophageal, or cloacal temperatures (on older chicks) were measured before and after respirometry with Wesco and Schultheis rapid registering mercury thermometers.

Attempts were also made in 1972 to measure chick body temperatures in the field, in order to determine typical core temperatures of freely foraging, brooded, and apparently cold-distressed young of different ages. Since each measured temperature first required a long period of quiet observation of chicks and adults in a group, relatively few observations were made.

Wild birds of known and unknown age were frequently recovered from small mammal snap-traps and were used for measurement and carcass analysis. Other reported weights for wild young of known age come from hand captures of banded birds, and field weighings with a series of Pesola spring balances.

## RESULTS AND DISCUSSION

Indoor captive alpina chicks furnished the most complete estimates of measures of growth (Fig. 2). Weight increase was sigmoid in form, attaining a daily mean of 1.73g over the 13-day linear portion of the curve (5th-18th day). Bill length increased steadily from hatching to the age of 20 days. The tarsus, however, was 90% of adult length at hatching, and virtually full size by the age of 5 days, a pattern in marked contrast to that of some altricial young (cf. Kahl, 1962). The emergence and rapid growth of primary feathers did not begin until the 10th day. These phase relationships are probably typical of nidifugous shorebird chick growth (cf. Soikkeli, 1967) although indoor captives attained juvenile weights of only about 80% of normal wild alpina young.

An energy budget for indoor captive alpina was formulated on the basis of monitoring the diet, respirometry, weight gain, and the caloric value of body tissues and excreta. Figure 3 shows this energy budget by day, and Table 1 summarizes the cumulative energy budget for captive alpina to the age of 21 days (approximate fledging age).

Extrapolation from captive to wild alpina chick energy requirements for the pre-fledging period is made on the basis of reasoning as follows: For captive chicks:

TABLE 1. Energy budget of laboratory-reared Calidris alpina chicks to the age of 21 days.

Gross Energy[1]
570 kcal

Metabolized Energy[2]
324 kcal

Maintenance Energy[2]
264 kcal

Resting Metabolism[1]
176 kcal

Excretory Energy[1]
246 kcal

Productive Energy[1] (stored as biomass)
60 kcal

Work[2] (exercise, activity, etc.)
88 kcal

[1] Values directly measured

[2] Values derived: Metabolized = Gross - Excretory
Maintenance = Metabolized - Productive
Work = Maintenance - Resting

Figure 2. Phase relationship among various measures of growth in indoor-reared C. alpina chicks. (Wing: flattened primaries; culmen: exposed length).

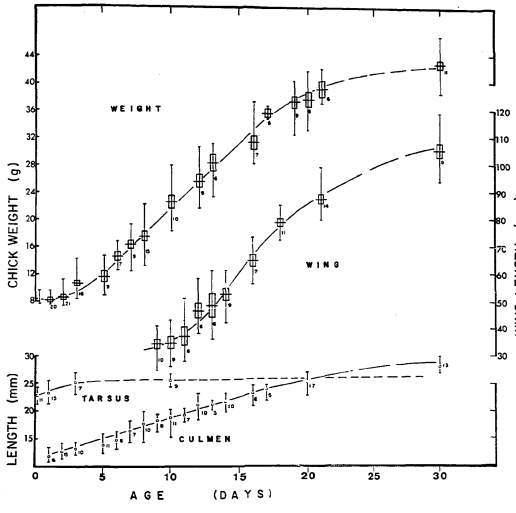
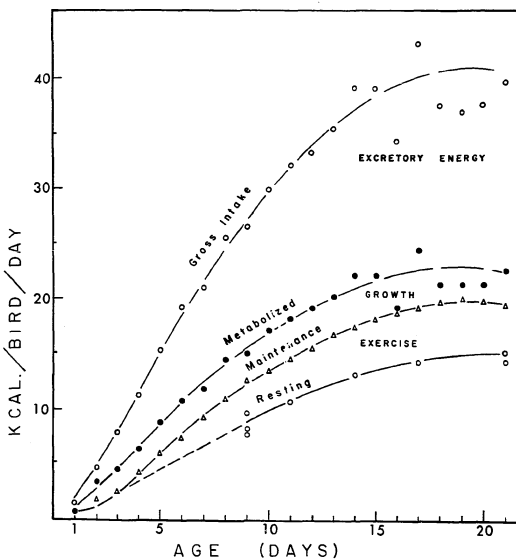


Figure 3. Energy budget by day, of pre-fledging indoor-reared *C. alpina* chicks.



Mean gross caloric intake for indoor laboratory chicks totalled 570 kcal over 21 days.

Metabolizable energy (gross minus excretory energy) was found to be 57 per cent of gross intake energy, or 324 kcal.

Productive energy, or the mean number of grams of biomass added (31.1g) multiplied by the average caloric value per gram of live weight (1.94) was 60 kcal.

Existence energy is defined as metabolizable energy (324) minus produtive energy (60), or 264 kcal.

Resting metabolism is derived from respiratory metabolism measurements made at temperatures within the presumed zone of thermoneutrality (35°C), and with the conversion factor that each liter of oxygen consumed produced 4.6 kcal of energy. By assuming that the average weight of the bird during the interval 0-21 days was halfway between hatching and fledging, the mean weight was 23.6g, corresponding to about an 11-day-old bird. The resting metabolic rate of an 11-day-old bird was about 4.5 cc $O_2$/g·hr or 11.7 kcal per bird per day, but some of the oxygen consumed is used in synthesis and growth. This energy may be presumed to equal the energy stored as biomass (Kleiber, 1961:316). Subtraction of the energy stored as biomass (PE) on day 11 (3.3 kcal, from Norton, 1970a:Fig. 8a) leaves the resting metabolic rate, 8.4 kcal per day (3.1cc $O_2$/g·hr), which gives a total for the 21-day pre-fledging period of 176 kcal.

Work energy (including energetic cost of biosynthesis) is estimated

by subtracting resting metabolism (176 kcal) from existence energy (264 kcal) to give 88 kcal. (See Table 1 for summary).

For wild chicks:

Proceeding in the opposite direction, we may estimate that work energy is twice as great as in the captive chicks. This estimate may seem low, but observations indicated that captive chicks, in in pacing to and fro in their cages, covered as much as 0.25km in linear distance per day, a distance of the same order of magnitude as that observed in the wild (cf. Holmes, 1966a:23). Wild chicks therefore expended some 180 kcal in muscular activity before fledging.

Resting metabolism must be estimated in reference to ambient temperatures on the tundra, which were about 5°C on the average, between 1 and 20 July. At 5°C, all chicks, wild and captive, were found to consume oxygen at maximum rates -- about 8.5cc $O_2$/g·hr, or 27.6 kcal/day for an 11 day (half-grown) chick. In resting metabolism, wild chicks expend 21x27.6 = 580 kcal. Some of the requisite heat production is provided by brooding adults or by calorigenesis of food (S.D.A.) and heat evolved in exercise so the resting metabolism for wild alpina may be set at a total expenditure for 21 days of life as 400 kcal.

Existence energy of wild chicks will equal resting metabolism (400 kcal) plus muscular work energy (180 kcal) or 580 kcal.

Productive energy is estimated by correcting for the estimated mean caloric value of wild chicks for this period (1.7 kcal/g live

weight -- Norton, 1970a) and multiplying by 1.25 times the productive energy of captive chicks, giving 66 kcal.

Metabolizable energy represents the sum of existence (580) and productive energy (66), or 646 kcal.

Gross caloric intake is estimated from metabolizable energy by using a factor expressing digestive efficiency, which for lab chicks was 57 per cent.

Estimated metabolizable energy of wild Dunlin chicks (646 kcal) represents 57 per cent of 1135 kcal.

In other words, a wild C. alpina chick requires an estimated 1135 kcal of tundra insect biomass over a 3-week period between hatching and fledging.

The 1968 indoor alpina and bairdii rearing resulted in an estimate for gross digestive efficiency of 57% (kcal metabolized/kcal ingested). Productive efficiency (kcal of biomass produced/kcal ingested) was 10%.

The slow growth, seemingly low measures of efficiency, high fat indices (Fig. 4) -- all were parallel to findings of Kleiber and Dougherty (1934) who raised domestic chicks at different temperatures. In addition, I suspected that the poor thermoregulatory capacity of captives was partly an artifact arising from high temperature rearing (Norton, 1970a).

Chicks reared outdoors had significantly higher rates of growth in both species (Fig. 5) regardless of whether they were kept individually or communally. The fat indices of outdoor-reared chicks were indistinguishable from those of wild birds (Fig. 4). Outdoor captives became capable of flight at the expected ages of 17-19 days in bairdii (N=4) and 19-22

Figure 4. Fat indices of indoor-reared alpina and bairdii chicks compared to those of wild, and outdoor-reared captives in these two species. Crosses next to values at or below 1.0 indicate that chicks may have died after depleting fat reserves, as when injured, but not killed outright, in small mammal snap traps.

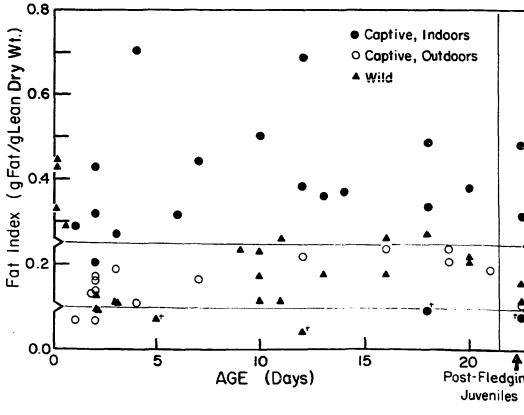
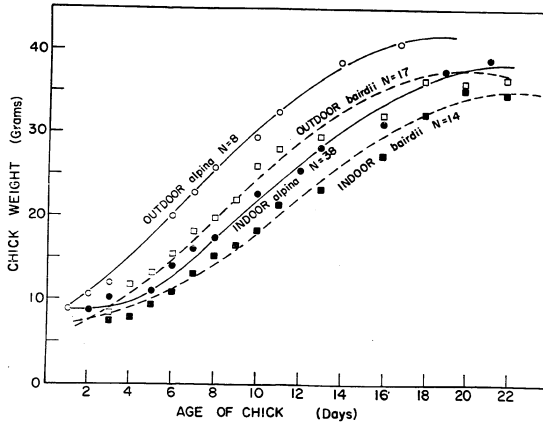


Figure 5. Comparison of mean daily weights as a function of age in indoor vs. outdoor captive populations of alpina and bairdii chicks.



days in alpina (N=3). No measures of digestive efficiencies or ontogeny of thermoregulation were made on outdoor captives. Birds in the communal pen, however, spent most of the time in the brooder, and an interruption in electric power for 4 hr killed all but the four oldest birds then in captivity.

The observation that one- and two-day old chicks in the wild could forage for periods of 30 min or more, at ambient temperatures of 0-5°C led me to assume that they were conventionally normothermic at much younger ages than indoor captive alpina. I further blamed the inability of the indoor captives to maintain a body temperature of 30°C at a chamber temperature of 15°C until the age of 10 days, on the darkness of the test chamber and their tendency to fall asleep during a metabolism run. Availability of wild bairdii broods for respirometry in 1972 changed these assumptions. The lighted chamber was effective in preventing the birds' falling asleep, but again, they became hypothermic at temperatures from which they had just come. The results of respirometry at different temperatures on 1972 bairdii chicks are shown in Figure 6. Downward-pointing arrows indicate that the chick was giving distress notes, its core temperature was below 30°C, or both. In light of these findings, we attempted to measure wild chick body temperatures during the remainder of the 1972 field season. The results, shown in Table 2, suggest that a core temperature of 30°C is about the level below which chicks are generally found to give distress calls, and to be dysfunctionally sluggish. Even the older chicks in the wild showed a surprising thermolability. We were not satisfied that we observed the maximum body temperatures

Figure 6. Oxygen consumption as a function of temperature and age in wild bairdii chicks in 1972. Curves are eye-fitted to values from chicks of known age, and the regression of adult bairdii metabolism on temperature is shown for comparison. Downward-pointing arrows signify that the chick's body temperature fell to below 30°C during the experiment, as determined by measurement immediately following the experiments. Data points without arrows indicate only that $T_b \geq 30°C$ at the end of the experiment, ranging as high as 41°C.

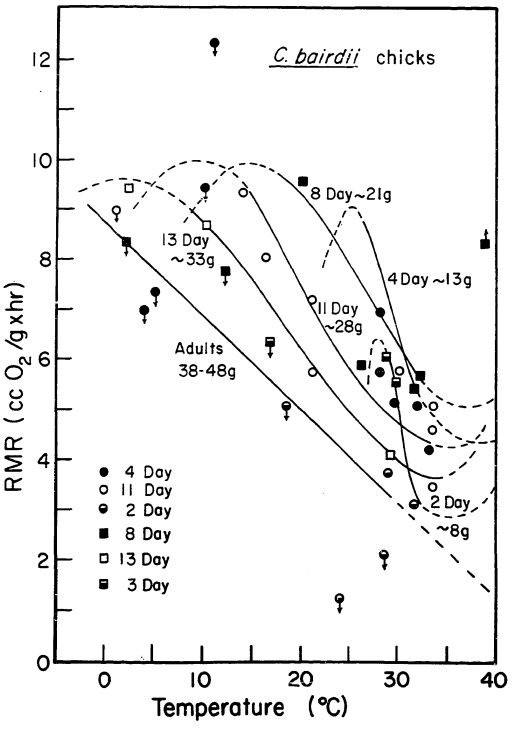


TABLE 2. Body temperatures of wild Calidris (alpina, bairdii, melanotos chicks under different conditions at Barrow.

| $T_b$ brooded[1] | | | $T_b$ feeding[2] | | | $T_b$ "distressed"[3] | | |
|---|---|---|---|---|---|---|---|---|
| N | Mean | Range | N | Mean | Range | N | Mean | Range |
| 6 | 37.2 | 33.5-38.8 | 11 | 34.3 | 29.5-37.5 | 17 | 28.6 | 22.5-30.5 |

[1] Chicks caught after adult disturbed from a brood observed attended for $\geq$ 5 min.

[2] Chicks caught after period of observation of $\geq$ 5 min. during which they continually fed, with adult(s) at hand, but not brooding.

[3] Chicks which were found only by distress calls, generally having been immobilized by parental warning upon observer's approach.

attained by chicks while being brooded.

Ambient temperatures at Barrow varied from season to season. Optimal weather conditions, including high temperatures, windless and sunny conditions, coincided with the peak of shorebird hatching in 1972, and continued almost without interruption through July and into August. A few recaptures of both melanotos and bairdii provided weight data on young of known age (Fig. 7) which suggest optimal growth in comparison to other years. Outdoor captive bairdii grew as fast, or slightly faster than their wild counterparts in 1969 and 1970, but the growth rates of 1972 wild bairdii were substantially higher than those of the best outdoor captives. Age of fledging in alpina, bairdii and melanotos was not observed in 1972, so it is impossible to say whether growth to that stage was completed correspondingly quicker than in other seasons, or whether the chicks were simply carrying extra energy reserves at a given stage of development. These species were more difficult to observe and recapture in 1972 than in other seasons, which I regard as indicative of behavioral fitness in consequence of physiological fitness.

A method for comparing growth rates in populations of young whose ages are not known, was suggested by Holmes' (1966a:Fig. 7) treatment of alpina growth at Barrow. He plotted arithmetic weight against logarithmic date to get a straight linear regression expressing growth rates. Figure 8 compares species growth rates, 1968-71 at Barrow. Also shown are data kindly provided by Professor Holmes for the 1962 alpina young, so that a uniform treatment, and comparison of data could be made. The samples from this study for each regression line included chicks of

Figure 7. Comparison of weight gain by bairdii and melanotos chicks in 1972 with values from other seasons.

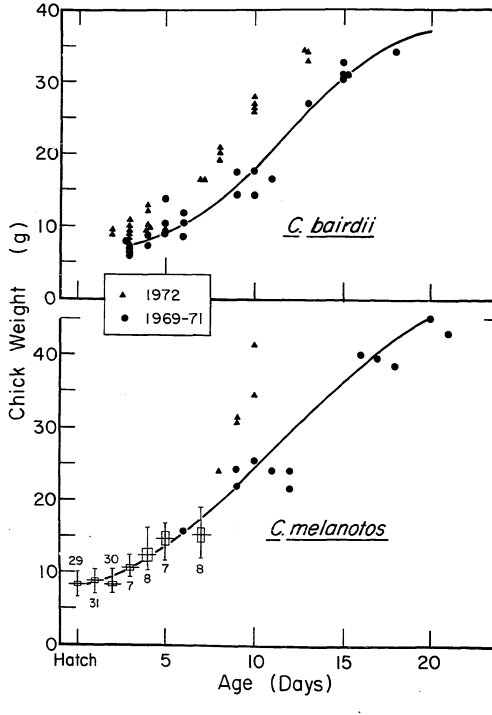
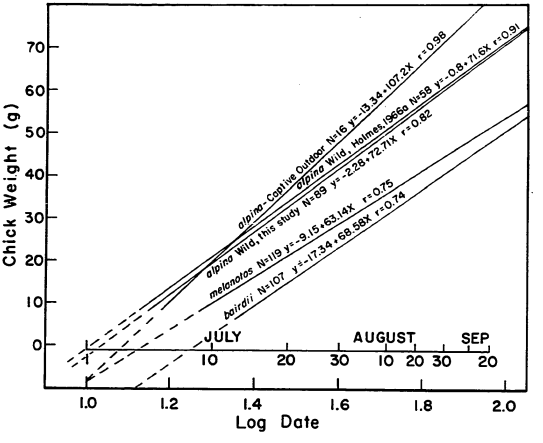


Figure 8. Graphic method for comparing growth rates of different chick species whose ages are not known. In this system, day 1 (=y intercept, or log date of 0) was considered to be 21 June, because a few alpina hatched before the end of June. Slope of the regression estimates mean chick weight gain for the interval log = 1.0 to 2.0, or 90 days.



known and unknown ages, but included only birds obviously beyond the day of hatching. This expression of growth rates is insensitive to possible seasonal differences in individual growth rates, but is highly sensitive to population synchrony, and relative dates for median hatching within a given species. Outdoor captive alpina (Fig. 8) illustrate this point. Data on their weights were normalized, such that each of 16 mean daily weights were adjusted to the date appropriate if all chicks had hatched on 4 July (median hatch date for alpina -- Norton, 1973a). The steep regression and high correlation coefficient result from this normalization. Wild alpina are relatively synchronous in breeding, and the two curves (which are statistically indistinguishable) for different cohorts of alpina bear this out. By contrast, melanotos, which individually grow somewhat faster than alpina, are shown to be less synchronous in hatching date. The bairdii curve also indicates population asynchrony, not as pronounced as in melanotos. The 1972 bairdii (not included in Fig. 8) despite their greater weights at a given age, yield a regression expression:

$$Y = -14.10 + 69.44x \; : \; r = 0.57 \; (N=31),$$

which is not significantly different from that of other years. Another feature of this treatment of growth is that the solid line in Figure 8 begins at the mean hatching weight for each species, which should correspond on the abscissa to the median hatching date. Correspondence obtains, within 1-2 days, as observed median hatching dates are 4, 9, and 14 July for alpina, melanotos, and bairdii, respectively.

Growth of sandpiper chicks at Barrow is shown to be temperature-

related in a complex manner: captive chicks did not grow well when forced to remain at 25-30°C, yet appeared to grow optimally during a long period of above average Barrow ambient temperatures. Wild chicks during the pre-fledging period were seen to be perfectly functional at body temperatures as low as 30 0°C, yet incapable of maintaining core temperatures above that level in the confinement of a respirometry chamber, until a surprisingly advanced age (cf. Obaldiston, 1966).

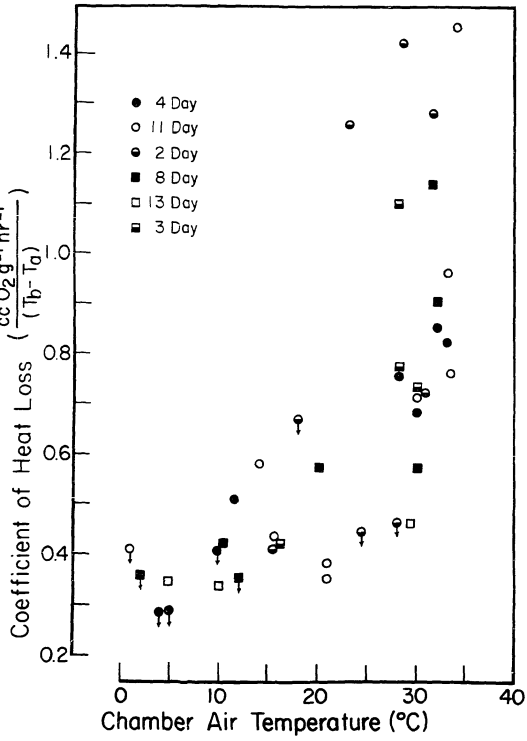
To assess the ecological requirements for energy by chicks, we first need a functional interpretation of the energy sources in the chicks' thermal environment. The available evidence suggests that chicks feed continuously so long as the effort (walking and pecking) is rewarding. Interruption of this routine occurs when prey items are not captured often enough, or when a predator's appearance causes adult alarm and protective immobility in the chicks. In either event, single immobile chicks normally lose heat faster than their resting metabolic rates can compensate for heat loss, and once below the apparent critical core temperature of 30°C, parental brooding is required. I conclude that locomotion evolves sufficient byproduct heat to maintain body temperatures, despite the probable decrease in effective insulation associated with exercise (Hart and Heroux, 1955). Exercise energy may be either additive to, or substitutive for, thermogenic increase in resting metabolism. Hart and Heroux (1955) found it to be additive in lemmings (Dicrostonyx) and rabbits. Pohl and West (MS) on the other hand found partial compensation in redpolls (Acanthis flammea).

Another, and probably substitutive, source of heat in the chicks'

energy blance is the calorigenesis, or heat increment of feeding ("specific dynamic action"), which Kleiber and Dougherty (1934), Kleiber (1961), Obaldiston (1966), and Norton (1970a) have all discussed in relation to growing birds. We lack concrete evidence for the magnitude of the heat increment of feeding, since it was impractical to fast chicks prior to respirometry, and no comparison between fasted and fully fed chicks exists here. The similarity between results reported here and those of Kleiber and Dougherty (1934) in both temperature-related growth rates and fat indices, suggests that productive efficiency and growth rates are optimal at mean temperatures between 10 and 20°C, largely due to the compensatory calorigenic effect of food. The insect diet of these sandpiper chicks, moreover, is presumably protein-rich, and maximally effective in producing the heat increment (cf. Kleiber, 1961). Interpretation of resting metabolic rates in an energy budget estimation for adult sandpipers treated the calorigenic effect as "internal productive energy" (Norton, 1973b) in birds living below thermoneutrality, and this condition applies equally to chicks.

Heat loss coefficients (more conventionally termed thermal conductance) may be derived from resting metatolic rates of the 1972 bairdii chicks (Fig. 9). Despite body temperature variations, heat loss coefficients appear to behave similarly to those of other, more stenothermal homeotherms (cf. Hooper and El Hilali, 1972; Miller, pers. comm.). The mean value for sandpiper chicks of different ages, below 20°C ambient is 0.421cc $O_2$ $g^{-1}$ $hr^{-1}/(T_b-T_a)$, or 1.94 cal $g^{-1}$ $hr^{-1}/(T_b-T_a)$. This value is 2.4 times that reported for adult redpolls averaging 13.9g (West, 1972),

Figure 9. Coefficients of heat loss in 1972 wild bairdii chicks of different ages, as a function of temperature. Symbols as in Figure 6.



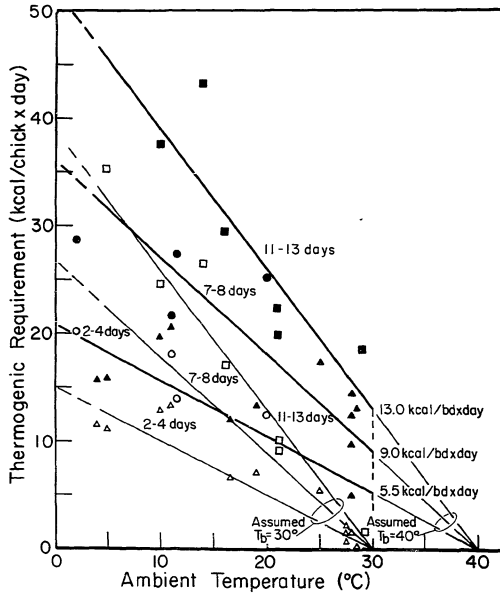
and 40% greater than predicted by Herreid and Kessel (1967) for 10g birds (dead, with plumage intact). Adult bairdii heat loss coefficients were lower by as much as a factor of 4, when measured in the same system as the chicks. Gessaman's (1972) estimate for Barrow Snowy owl heat loss coefficients of 0.05 cal $g^{-1}$ $hr^{-1}/T_b-T_a$ are, in turn, an order of magnitude lower than those for adult bairdii. Despite the questionable theoretical basis underlying application of the Newtonian model for cooling in supposedly heat-losing, but not cooling, homeotherms (cf. Kleiber, 1961; Calder, 1972), differences of such a magnitude in estimated heat evolution justify at least cautious use of this, the most easily understood model available.

The Newtonian model predicts that metabolism must keep pace with heat loss in a homeothermic system, as expressed by:

$$M = C\ (T_b-T_a)$$

where M is metabolic rate, C is coefficient of heat loss, $T_b$ and $T_a$ respectively body and ambient temperature. This formula may be used to determine the thermogenic requirements for chicks at different ages, while artifically setting $T_b$ at different levels. The thermostatic heat requirements are estimated for whole bird metabolism in Figure 10, based on measured heat loss coefficients derived from the respirometry experiments (Figs. 6 and 9) on these birds. This graph shows that a 10°C difference in lower allowable $T_b$ is reflected in metabolizable energy requirements for single birds. A body temperature set at 30°C theoretically lowers by 13 kcal/day the metabolized energy necessary to keep an 11-13 day old bairdii chick at thermal equilibrium. This rough estimate

Figure 10. Estimated requirement for metabolic thermogenesis in 1972 wild bairdii chicks at three different stages of development. The differences in requirement are estimated between theoretical cases of thermolability ($T_b$ = 30°C) and stenothermy ($T_b$ = 40°C).



predicts a thermal deficit for 11-day chicks below about 10°C, even at maximum resting metabolic rates, and requiring only $T_b$ of 30°C. This estimate further emphasizes that heat must be derived from other sources than resting metabolism during activity of chicks at normal Barrow environmental temperatures.

As temperatures drop daily, or during bad weather, the likelihood of brooding is increased. For that reason, an exceptionally cold year, such as 1969, affords better chances of recovering whole broods of known age. Sampling chick weights during prolonged cold periods results in an underestimate of weight gain, not because brooding interferes with foraging time (cf. Theberge and West, MS) but because it is symptomatic of unsuitable foraging conditions. In 1969, for example, I captured two bairdii chicks weighing 11 and 14g at the age of 21 days (cf. Fig. 8).

The physics of brooding is unknown. We may assume that the energy cost of brooding per se to the adult(s) involved is not great. Although adult vascularized brood patches persist, much of the heat requirement of the chicks is reduced by the simple increase of insulation afforded by parental contour feathers, and the huddling of more than one chick together optimizes their mass-to-surface ratio (cf. Royama, 1966; Mertens, 1967).

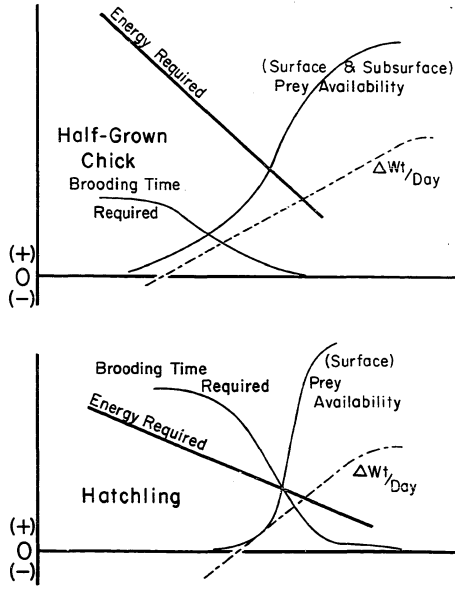
The temperature at which brooding is necessary declines with age at an unknown rate. As chicks develop harder and longer bills, they are capable of increased reliance on subsurface arthropods, indicated behaviorally by a pronounced inclination of laboratory-reared chicks to probe in wet sand.

The relationships of these processes are shown schematically in Figure 11. The amount of brooding time required per chick no doubt declines with age at a given temperature. On the other hand, increased size, mobility, and dispersion of a brood may require increasing amounts of the adult's time if individuals must be brooded successively rather than simultaneously.

Heterothermous operation of tissues among animals broadly classified as homeotherms is most often regarded in terms of energy conservation. Regional heterothermy and associated vascular reflex systems are specifically heat-conservative (cf. Irving and Krog, 1955), while whole body cooling in cases of torpor and hibernation allow more general energy conservation (cf. Lasiewski, 1963; Mullen, 1971). Precedent therefore exists for considering thermolability as adaptive energy conservation in small birds, and this consideration has properly been extended to the thermolability of altricial neonates (Breitenbach and Baskett, 1967; Dyer, 1968). Precocial and nidifugous sandpipers, however, are shown here to share thermolability with altricial nidicoles. The thermolability of sandpiper chicks is instructive, because it cautions us against taking for granted a rigid physiological distinction between altricial and precocial growth modes among young birds. Koskimies (1962) and Bernstein (1973) have shown that precocial gallinaceous birds may be incapable of endothermy until nearly fledged, but the thermal gradients naturally faced by the species they considered were small by comparison to arctic sandpiper chicks.

The thermolability described here for chicks represents an extension

Figure 11. Schematic representation of changes in energy required, brooding time required, the availability of insect prey, and weight gain as a function of ambient temperatures, between hatchling and half-grown chick stages in Calidris species.




Ambient Temperature

of the characteristic from the egg stage, as I have described elsewhere (Norton, 1970a; MS) the adaptive survival of extreme chilling (naturally and experimentally) by Calidris embryos.

Hibernation and torpor in mammals and birds may be more striking examples of energy conservation than is chick thermolability, but the physiological and intermediary metabolic problems of Calidris chicks undoubtedly would bear closer examination along the lines of the many investigations of those better known phenomena. For example, do nerve conduction velocities behave like those of hibernators or uninsulated extremities of mammals (cf. Miller, 1967; Miller and Irving, 1967)? The enzyme systems of Calidris chicks also deserve study in relation to temperature optima, concentrations in critical tissues, etc. (cf. South and House, 1967).

Growth rates of 1972 chicks, about which additional data should be forthcoming from Safriel (pers. comm.) and Pitelka and Remsen (pers. comm.) suggest the overriding importance of climate, particularly temperature, in the outcome of the yearly "reproductive gamble" made by breeding adults. The warmer than average, sunny weather began at the end of June in 1972, and resulted in a prompt emergence of adult tipulid and chironomid insects, as described generally by MacLean and Pitelka (1971). The rate of emergence had peaked and abated before the first Calidris eggs hatched, and at that point MacLean (pers. comm.) speculated that the sandpiper chicks would bear very close watching when they hatched, since they would apparently be forced to depend on a small proportion (e.g. 10%) of the total potential seasonal biomass of ephemeral adult insects. Perhaps in

a "normal" year MacLean's implied forecast of widespread undernourishment and mortality would have been borne out. The continued balmy weather, however, appeared to reduce the time required in brooding to such an extent that chicks foraged virtually without interruption on the remaining adult insects. This success indicates that weather is incomparably more important in the outcome of the annual reproductive gamble by shorebirds in the Arctic, than is competition for resources between chicks of different species, or between adults and chicks.

All but the two passerine species breeding at Barrow have precocial young (Maher, 1964). Kahl (1962) was impressed by the rapidity and ecological efficiency of the altricial mode of growth in the Wood stork (Mycteria americana), but did not consider the energetic contribution required of both adults in his estimation of ecological efficiency. The prevalence of the nidifugous habit is typical of open country (i.e. 2-dimensional habitat) and ground-nesting species. This study suggests that persistence of thermolability represents an adaptive specialization of the precocial physiological system allowing greater efficiency of growth in cold environments.

In spite of the theoretical metabolic economy achieved by thermolability, there may be other energy sources required by the growing chicks. In addition to heat evolution from muscular activity and the calorigenic effect suggested above, radiant energy may substantially reduce net thermolysis at times. Heppner (1970) found that metabolism of black-feathered birds would be some 20% lower than that of white-feathered birds. The magnitude of this difference suggests that the phenomenon should be investigated in reference to levels of radiant energy at Barrow.

# CHAPTER 5.

# SYNTHESIS: ECOLOGICAL ENERGETICS OF CALIDRIDINE SANDPIPERS BREEDING AT BARROW, ALASKA

## INTRODUCTION

Multiplication of individual metabolic requirements (Norton, 1973b,c) by population densities and residency values for different species (Norton, 1973a) allows us to estimate the seasonal community energy requirements for calidridine sandpipers breeding at Barrow. These requirements may then be used in exploring the interactions of shorebirds with the tundra arthropods which support the entire breeding effort (cf. MacLean and Pitelka, 1971). The derivation of estimated requirements, and evaluation of the impact of shorebirds on their food resources serve to identify further questions about the short term effects of resource levels upon breeding densities, and about selective advantages of different patterns in allocation of breeding efforts.

The field of ecological energetics is relatively new, and therefore a number of distinct analyses and discussions could appear under the title of this section. It is to be hoped that others will, in fact, appear because the strategy of insectivory by arctic-breeding calidridine sandpipers is susceptible to analysis, as are other aspects of these species' breeding biology. The volume of Calidris studies preceding and facilitating this synthesis supports that assertion (cf. Pitelka et al, MS).

Although we tend to regard arctic ecosystems as simple, this is accurate only in a relative sense. The considerable complexities surrounding the single transfer function between arthropods and shorebirds dictated further simplifications for the purposes of the discussion which follows. For example, only the two insect species most heavily preyed

upon by sandpipers at Barrow are considered in any detail. This simplification and others are sacrifices of resolution, in the interests of making the dynamics of trophic relations as clear as possible.

## METHODS

Estimates of tundra residency (bird-days/ha) are multiplied by daily caloric requirements estimated for each species on the basis of respiratory metabolism studies (Norton, 1973b,c), and on further reasoning outlined below.

Impact on tundra arthropod resources is estimated for each species separately, and for the group as a whole, for prey items of different sizes. The required rate of prey capture is estimated as a function of energy requirement, foraging time available and prey size. Caloric equivalences are assumed, as follows: 4.6 kcal/liter $O_2$ consumed (Kleiber, 1961); 5.5 kcal/g dry weight of arthropods (MacLean, pers. comm.); adult mean digestive efficiency of 0.8 (cf. King and Farner, 1961); chick mean digestive efficiency of 0.6 (cf. Norton, 1970a).

## RESULTS AND DISCUSSION

The expansion and extrapolation of respiratory metabolism measurements to estimates of population food requirements from the tundra ecosystem may be approached variously. One way is by piecing together a day-by-day estimate of caloric requirements based on the stage of breeding, and on identifying energy use by individuals at each stage (e.g. West, 1960; Brenner, 1968; West and DeWolfe, MS). I reject this approach for

the data available, because the apparent precision of the estimate would be illusory. Adults were only trappable on the nest, which leaves us to extrapolate about their metabolic performance, both before and after the nesting period (egg-laying through hatching).

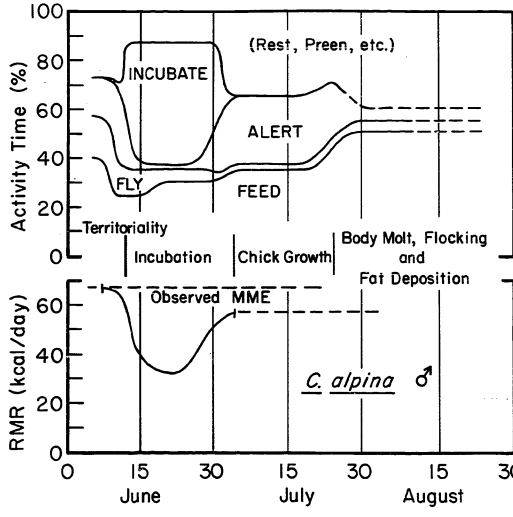
An alternative approach is to estimate a single daily average requirement for calories of arthropods ingested, to be multiplied by estimates of tundra residency. This approach is not only elegant at the outset, but will facilitate later corrections as we learn more about energy and time use by free-living birds. The question becomes one of establishing the credibility of a single mean daily requirement. This single value should be easily derived, susceptible to re-examination, and be comprehensible to investigators dealing with other components of the ecosystem. For these reasons, I choose to assume for this discussion that Calidris sandpipers at Barrow are exploiting tundra arthropods at a rate which allows them to mobilize energy at maximum rates throughout their residence at Barrow.

Resting metabolic rates (RMR) of Calidris adults were found to be maximal at ambient temperatures just above those at which the birds became hypothermic and developed bradycardia (Norton, 1973b:Fig. 1). Maximum RMR theoretically represents maximum metabolizable energy (MME), a rate ceiling for long-term energy mobilization (Kendeigh, 1949, 1969b; West, 1960; Kontogiannis, 1968) specific for any homeotherm on a particular photoperiod. By specifying long-term, I mean to focus attention on the daily interval, over which birds may mobilize energy at higher rates for brief periods, as during flight, but must replace the deficit so as not

to sustain a loss of energy reserves. Values for MME were obtained at temperatures between -10 and -24°C for alpina, bairdii, and pusilla. The MME for melanotos females appeared to be at least 20% higher than that for alpina females, because three birds tested for 30 min each at chamber temperatures of -29 to -34°C all failed to show declines in oxygen consumption, heart rate, or body temperature.

The use of maximal estimates for these species may not overestimate their true energy requirements. Wiegert (1968) has argued on thermodynamic grounds that indirect calorimetry may substantially underestimate the energy requirements of productively active natural populations. The continuous daylight at Barrow during the breeding season permits adult birds to remain active a large proportion of the time, hence presumably operating at higher than resting levels of energy requirements. Maximal requirements for metabolized energy seem, furthermore, to occur during most of the breeding season. Figure 1 illustrates the adjusted RMR observations on an idealized male alpina, in which the clutch is completed on the median date for the population (12 June) and the eggs hatch accordingly on 4 July. RMR for the nesting period is expressed in kcal/bird·day, and is adjusted to appropriate levels for mean daily ambient temperatures occurring between 12 June and 4 July. During egg-laying male alpina (as well as female alpina and melanotos) were all estimated to be using their full metabolic potential (Norton, 1973b). Information about the breeding cycle and productive activities during tundra residence late in the season are expressed in Figure 1. The upper section presents an hypothetical time-activity profile for

Figure 1. Summary of observed metabolic rates (RMR), known breeding season activities, and hypothesized partial time-activity budget for an idealized male alpina. Solid line represents extent of measured RMR, corrected for Barrow ambient temperatures on the dates indicated, which represent median values for dates of onset of incubation, etc. -- see text.



alpina. Although no timed activity observations were made in these studies, except that of incubation effort (Norton, 1972), the partial profile presented here represents the best guesses of three students of Calidris biology (MacLean, Safriel, and myself) and of T. W. Custer, who has made timed activity observations on Lapland longspurs (Calcarius lapponicus) at Barrow. These estimates were formalized at Barrow in 1972.

The relevance of the estimated activity budget and the processes listed in Figure 1 lies in the energy cost of the activities and processes shown. Tucker (1968) and Gessaman (pers. comm.) found that sustained flight in a wind tunnel requires 8-12 times the resting metabolic rate. When the percentage of time spent flying is high, as during territorial establishment by male alpina, the daily caloric requirements can be expected to reflect this demand. Likewise, alertness probably raises energy-demands and I believe alertness can be distinguished metabolically (Norton, 1973b). Behaviorally, I consider alertness to be a wakeful, non-resting, and non-feeding state, characterized by a predisposition to give alarm notes and calls. An increase in alertness at the end of incubation was credited with the marked rise in RMR of birds at that stage, and it is expected that alertness remains high in chick-brooding adults until the young are fledged. Late season body molt, fat deposition, and increased flying are shown in Figure 1 to follow fledging in alpina (Holmes, 1966a; MacLean, 1969). Thus there are enough energy-demanding activities and processes during most of the breeding cycle to account for maximum metabolic rates in breeding birds.

Only the middle third of the incubation period itself is not seen to demand maximum metabolic rates. However, this is the period of theoretical maximum external productive energy demands, in the form of incubation, and therefore use of maximum metabolic rates even during this period may not overestimate the true situation.

Table 1 gives the gross energy requirements of each species population using MME values based on maximum RMR observed for each adult of each species. These values are multiplied by estimates of tundra residence per ha for each species, and for the group as a whole. Male and female alpina, along with post-fledging young, account for 1,750 kcal/ha seasonally, or 47.5% of the 3,692 kcal/ha estimated total Calidris requirement. These estimates are 4- and 5-year mean values, taking into account nest failures and chick mortality. In 1971, however, melanotos requirements made up a greater proportion than usual of the seasonal requirement, as did the bairdii population in 1969. The long-term mean values show alpina to be energetically the most important of the four species, because of its stable nesting densities, and the long residency of the population. But the excursions from the average are interesting in themselves. In 1971, the Calidris community is estimated to have required nearly 5,000 kcal/ha, of which 2,000 kcal/ha, or 40% went to melanotos; this species thus accounted for much of the 25% increase in the community requirement that year. The statistical problem posed by opportunism in this case is much the same as that posed by avian predators on lemmings at Barrow. Once every 4-5 years, Snowy owls and Pomarine

TABLE 1. Gross energy requirements per unit area (kcal/ha) of adult Calidris sandpipers at Barrow.

| SPECIES | | MME[1] (kcal·bd/day) | RESIDENCE[2] (bd·da/ha) | GROSS ENERGY[3] (kcal/ha) |
|---|---|---|---|---|
| alpina | ♂ | 67 | 10.0[4] | 835 |
| | ♀ | 73 | 10.0 | 915 |
| bairdii | ♂ | 52 | 6.6 | 427[5] |
| | ♀ | 60 | 4.2 | 315 |
| melanotos | ♂ | 110 | 3.0 | 422 |
| | ♀ | 86 | 3.7 | 397 |
| pusilla | ♂ | 39 | 3.8 | 185 |
| | ♀ | 44 | 3.6 | 196 |
| | | | Total: | 3692 |

1 based on maximum RMR at low temperatures (Norton, 1973b)

2 based on adult residence corrected for nest loss, etc. (Norton, 1973a)

3 assuming a digestive efficiency of 0.8

4 alpina values include residence of post-fledging young

5 bairdii males assumed to brood

jaegers may effect the single largest transfer of energy into the avian community. For these opportunistic species, population energetics studies must span a number of seasons, or a complete cycle of scarcity and abundance at one location, to assess their relative energetic importance.

Energy requirements of growing chicks can be estimated in reference to alpina gross energy requirements, estimated by Norton (1973c). Table 2 is an extrapolation based on the weight gain of each of the species relative to alpina chicks. The impact of all pre-fledging chicks per ha amounts to about 15% of that of adults and post-fledging juveniles (560/3,700 kcal per ha).

Using the derivations in Tables 1 and 2, the gross, or ingested energy requirements may be translated into numbers of prey items required. Figure 2 relates the number of prey items required per nesting attempt, to the mean size of prey captured. Figure 2 indicates, for example, that each nesting attempt by alpina (facing average expectancy of success, chick survival, etc.) accounts for as few as 100,000 prey items of mean biomass of 30mg dry weight. This is about the average value for Tipula carinifrons larvae ingested (MacLean, pers. comm.). If, on the other hand, alpina preferentially selected prey items averaging only 1mg dry weight, the number consumed per nesting attempt would be 3.2 million seasonally. Prey items of less than about 1.7mg, the value for adult Pedicia hannai (MacLean, pers. comm.) do not comprise a substantial proportion of the diet of adult or fledged young alpina (Holmes, 1966b).

The density of sandpiper consumption of prey items (no/ha) is shown

TABLE 2. Calculated gross energy requirements for Calidris chicks between hatching and fledging at Barrow.

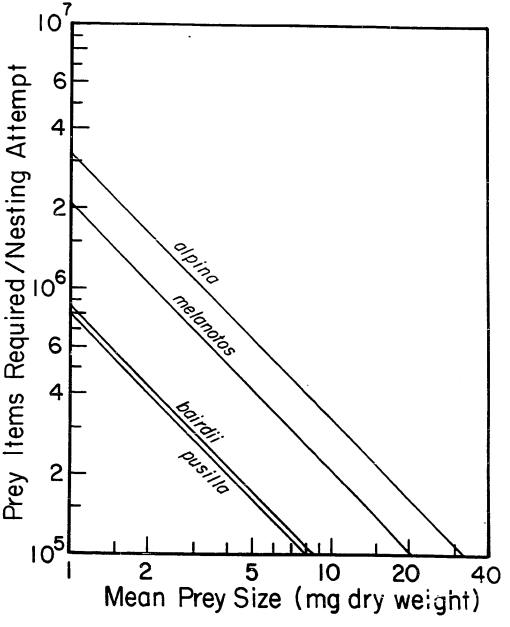
| Species | Weight gain (g)[1] | Ratio to alpina | Gross E (kcal/chick) | Chicks[2] fledged/nest | Density[3] (nests/ha) | Gross E (kcal/ha) |
|---|---|---|---|---|---|---|
| alpina | 49.5 | 1.0 | 1135 | 1.43 | 0.11 | 178.0 |
| bairdii | 35.9 | 0.725 | 822 | 0.76 | 0.18 | 112.5 |
| melanotos | 71.6 | 1.45 | 1640 | 1.4 | 0.09 | 206.0 |
| pusilla | [21.7] | 0.438 | 493 | 1.38 | 0.10 | 68.0 |
| | | | | | Total: | 564.5 |

[1] weight gained: $\left(\frac{\text{ad } \sigma + \text{ad } \varphi \text{ wt}}{2}\right)$ - mean hatching weight

[2] Assumed mortality of chicks: 50% between hatching and fledging; or $\left(\frac{\text{hatching success}}{2}\right)$; hatching success from Norton (1973a)

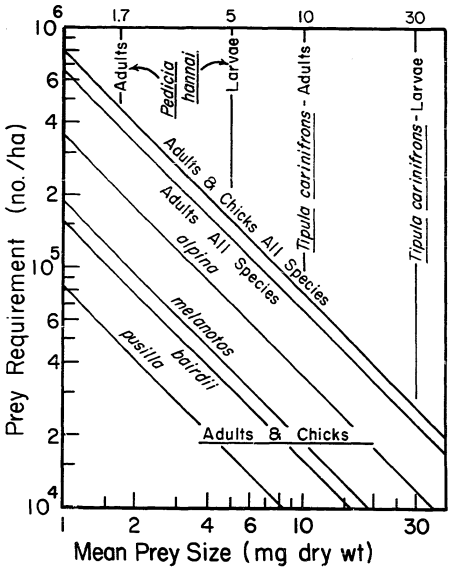
[3] Nesting density: an average of all Barrow annual averages (Norton, 1973a:Table 2)

Figure 2. Estimated requirement for number of prey items per nesting attempt as a function of the mean prey item size, in Calidris sandpipers. Values are estimated on the basis of nests begun with the mean probability of failure, predation, etc., for each species.



for each species and for the entire community, chicks included, as a function of mean prey size in Figure 3. The larval biomass values indicated in Figure 3 are based on weight:length regressions for each species, and on mean lengths of larvae found in Calidris stomachs (MacLean, pers. comm.). Although "mean prey size" for adults and chicks is in itself a datum of limited value, the significance of Figure 3 is its prediction of how many prey items per ha Calidris populations would require if the birds were perfectly selective, or monophagous, for any of these four prey items. It is worthwhile to explore some of the ramifications of these maximal estimates for insect prey required. For example, Figure 3 helps us to understand why monophagy among all members of the Barrow Calidris community, on either of the two adult insects shown, would not support the observed populations of birds. Even if adult insects emerged throughout the season (which is not the case -- see below) the requirement for all Calidris species would be $4.5 \times 10^5$ P. hannai per ha, of which only $2.7 \times 10^5$ emerged per ha in 1971 (MacLean, 1971). For T. carinifrons, the requirement would be $8 \times 10^4$ per ha, but only $5 \times 10^4$ emerged per ha in 1971. In other words, only 60-66% of the total community requirement could be supplied by adult insects of either species. MacLean and Pitelka (1971) demonstrated the other (and overriding) reason why these adult insects cannot support breeding Calidris populations, by showing the temporal synchrony of the emergence. Their data show that in normal years 95% of the short-lived adults emerge over 14-21 days in T. carinifrons, and 7-14 days in P. hannai. This population synchrony in insect emergence was ascribed to "predator

Figure 3. Density of estimated prey requirement (#/ha) for adults and chicks of each Calidris species, and of the entire community at Barrow, as a function of the mean size of the prey item ingested.



swamping" by MacLean and Pitelka (1971). The validity of their hypothesis rests on several conditions. First, the adult insects must be so overwhelmingly abundant during peak emergence, that all predation combined is insufficient to stop their successful mating and egg-laying. Second, Calidris sandpipers must be highly effective predators on surface insects both before and after peak emergence. This effectiveness is required in order to substantially reduce insect reproduction by the 5% of adults emerging early and late (the "tails" of the normal distribution). Just how effective this predation must be, is indicated by the short time (perhaps a few hours) elapsing between emergence and completion of oviposition (MacLean, pers. comm.).

One could imagine these trophic relationships operating in a qualitatively very different manner. If, for example, no sub-surface feeding specialists bred at Barrow, the seasonal emergence of adult insects might be greater in magnitude, and spread out over a greater proportion of the snow-free months. Whether adult insects alone could, or might ever have, supported breeding populations of birds such as presently make up the Barrow avian community is not certain. The modern populations that practice the strategy of arctic insectivory, however, are all forced to greater or lesser degrees, to be generalists in their feeding habits. Besides subsurface feeding by Calidris species, other examples of diversified feeding styles at Barrow are that of the Red phalarope, which can rely on aquatic arthropods; and that of partially granivorous Lapland longspurs (Custer, pers. comm.).

Adult insects are most available for some 15 days seasonally.

Adults of all four sandpiper species spend about 45 bird-da/ha on the tundra (Norton, 1973a:Table 5). We can therefore estimate that no more than 33% of the Calidris energy requirement is taken from the tundra in the form of adult insects. The use of adult insects is further reduced, however, by the departure of one Calidris adult in three of the four species at the time of hatching which optimally corresponds to the time of peak insect emergence. Just how much this departure reduces the predation on adult insects depends on several annual variables, including nesting densities of the three early-departing Calidris species (bairdii, melanotos, and pusilla), the coincidence of shorebird hatching and insect emergence, and survival of the chicks, which are virtually obligate predators on surface-active adult insects. Since pre-fledging chicks are estimated to require 15% of the annual adult energy requirement, this puts a lower probable limit on the community dependance on adult insects. It is probably not far afield to estimate that adults and young of the four Calidris species derive altogether about 25% of their total seasonal energy required from adult insects. The relative requirement and abundance estimates suggest that enough insects are available during emergence to make the proposed "predator swamping" mechanism work. If, for example, predation were equally distributed between P. hannai and T. carinifrons, the Calidris community would crop about 20% of the total emergence of each. Enough adult insects emerge and survive long enough to fertilize and lay eggs, insuring that a new cohort will reliably enter the species' larval population. Although insect emergence is cropped by additional species at Barrow, either regularly, as by Lapland

longspurs, or facultatively, as by flocks of wandering Longtailed jaegers (Stercorarius longicaudus), both of these species feed primarily on the larger T. carinifrons adults, and cannot, in any case, consume the 80% left them by calidridine sandpipers.

Dependence upon larval insects cannot be explored conveniently by reference to numbers of prey items, as in Figure 3, because Calidris adults prey selectively on the larger, later instar larvae, in which the greatest proportion of larval biomass is concentrated (MacLean, MS; pers. comm.). The total seasonal biomass requirement for Calidris populations would be 670 g/ha at the estimated mean caloric density of 5.5 kcal/g dry weight. If, as discussed and estimated above, 25% of the seasonal energy requirements of adult sandpipers come from adult insects, then 75% of the total, or about 500g/ha, would be removed as larval insects seasonally. This estimated biomass requirement allows us to explore estimates of tipulid larval biomass present through the breeding season (MacLean, 1970; 1971). His figures indicate that in 1970, between 1,230 and 11,750 g/ha of T. carinifrons larvae could be found in mesic and try tundra soils, and between 450 and 6,000 g/ha on wetter sites. By contrast, P. hannai larvae were less abundant on drier sites (0-410 g/ha) but more abundant on wetter sites (2,270-5,000 g/ha). There is, in short, an impressive standing crop of larval insects in relation to shorebird requirements, even though the soil sampling technique (Berlese funnel elution) produces a high degree of variability when expanded to estimates of biomass/ha.

If T. carinifrons predation is confined to drier sites, and

P. hannai foraging to the wetter sites by all adults, then calidridine sandpipers at Barrow might consume no more than 4 to 15% of the standing biomass of either insect species if we take the seasonal average estimates of MacLean (1970, 1971).

Another measure of calidridine sandpiper impact on tundra arthropods would be a comparison of arthropod production per ha with the estimated gross energy required by the birds. It is axiomatic that consumption by one trophic level cannot outrun production of the next lowest one. MacLean (pers. comm.) has provided a tentative figure for production by Pedicia and Tipula larval populations of 10,000 kcal/ha each at moderate densities. All Calidris adults might consume 2,700 kcal/ha, or some 13.5% of the annual production of each species, assuming equal distribution of predation.

These estimates are subject to further refinement, but at the present level of understanding we can make several comparisons. These shorebirds are estimated to crop perhaps 20% of the adults emerging seasonally, but only 4-15%, or 13.5%, of larval insect energy at their disposal. In view of the substantial error surrounding these estimates resulting from the long train of logic and assumptions behind their derivation, I feel justified in injecting my own plus and minus impressions on these estimates. I believe that the value of 20% effective predation on adult insects is low, because of what we see during warm days in the midst of emergence. The excreta voided by adults contain only partially dismembered bodies of adult Tipula and Pedicia when these are maximally abundant. It is as if the birds are

compulsive in their consumption of surface-active insects, and the consumption rate exceeds the rate of digestion. At other times, the excreta give no indication of consumption outpacing digestion. The question of digestive efficiency and its variability unquestionably deserve investigation, but these observations suggest that the birds consume more than they actually "need", and therefore may take more than the estimated 20% of adult insects emerging seasonally.

Shorebird predation appears not to take as high a proportion of the energy proffered by larval insects as it does of surface-active prey, whether measured in terms of the standing biomass of the two dipteran species, or in terms of estimated annual production. Great caution is warranted in assessing "availability" of prey for Calidris species, particularly that of larval prey. The subsurface mode of feeding for soil arthropods involves a set of sensory and behavioral mechanisms relatively more alien to our comprehension than does presumably visual detection and capture of surface prey. Eventually, we may discern some probabilistic function relating the effort of foraging to larval prey density. They are no doubt inversely related, and it is easy to presume that there is a point on this curve at which the individual bird begins to lose ground energetically. Most interestingly, there may be another, independent, point on the curve, at which the individual defects from the system by emigration. This second point on our non-existant function may vary widely, above and below the first point, depending on factors not clearly related to energetic variables, such as behavioral commitments to nesting in progress, young birds needing brooding, etc.

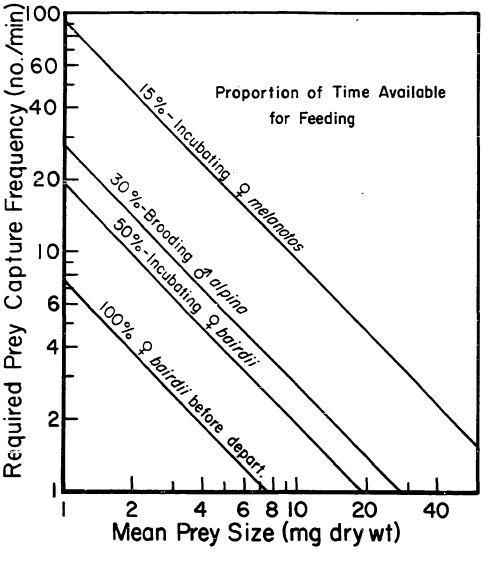
Figure 4. Estimated required prey capture frequency as a function of mean prey size, by members of the Barrow Calidris community, with varying amounts of time available for feeding.

For the purposes of evaluating "prey availability" Figure 4 shows how frequently various members of the Calidris community are required to capture prey items of different sizes in the time available for foraging. C. melanotos females during incubation, with only 15% of the day available (Norton, 1972) must capture 18.5 P. hannai larvae per min of foraging to afford maximum metabolizable energy. The credibility of this estimate could be tested (with some difficulty) in the field. From my observations of melanotos off the nest, their rapid and single-minded style of feeding in wet meadows and polygon troughs could reasonably be expected to yield a Pedicia larvae once every 3 sec at moderate to high densities of these soil larvae. Reliance on 1.7 mg Pedicia adults would require a capture rate by melanotos females of 55/min, or nearly one item per sec. By contrast, other members of the community can be, and in fact seemed to be, more relaxed in feeding, largely because the sharing of incubation allowed both adults more time for foraging. Brooding alpina, for example, may require only one Tipula larva per min of feeding effort, or 15 Pedicia adults per min, according to Figure 4.

With these relationships in mind, we can confront the several questions and hypotheses surrounding resource limitation upon breeding calidridine sandpiper populations. These bear re-stating at this point:

1. Do food resources proximately limit populations and breeding densities of arctic shorebirds?
2. Do energy resources act as ultimate controlling factors in the evolution of breeding strategies, as proposed by

Figure 4. Estimated required prey capture frequency as a function of mean prey size, by members of the Barrow Calidris community, with varying amounts of time available for feeding.



Pitelka et al. (MS)?

3. What additional information or succint questions concerning food resources utilization processes are indicated by this exercise?

The estimated maximal energy requirements of 4-5 yr means for Calidris populations at Barrow do not offer any clear defense of the idea that the density of prey itself controls the breeding density and productivity of breeding sandpipers. This discussion has focused on only part of the array of bird species dependent on these arthropods. It is possible that the proportion of standing biomass of both larval and adult insects consumed by all insectivorous species at Barrow is somewhat higher than the 10% generally expected for the gross transfer of energy from one trophic level to the next (cf. Phillipson, 1966). The trophic dynamics at Barrow may be unusual in this regard. MacLean (MS; pers. comm.) finds that life cycles of the two insect species discussed here both take 4 or more years to complete at Barrow. From the point of view of the shorebirds, this prolonged life cycle affords an attractively high level of standing larval biomass. At Prudhoe Bay, where soil temperatures are higher, insect life cycles may be shorter, which would result in a less attractive ratio of biomass to productivity for shorebirds. Censusing of breeding avifauna at Prudhoe Bay reveals lower breeding densities of these same Calidris species (Norton et al., in prep.) with no significant inclusions in the community there of other species populations which might compete for similar resources. This finding suggests first that a low productivity to biomass ratio

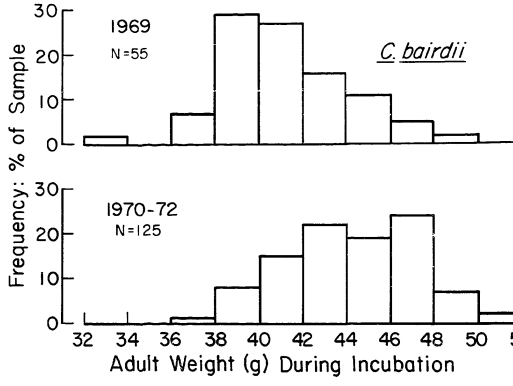
is ideal for the general strategy of arctic insectivory, and second, that some evidence for proximate limitations on arctic shorebird populations may be sought by such inter-site comparisons.

Watson and Moss (1970) observed that the concept of resource limitation of biological populations has been inherited from the physical sciences, in which reaction rates may be precisely controlled by limiting substrate concentrations of the reactants. In biological systems, we are apt to come to grief by assuming that the same precision applies: food, or the parallel to substrate concentrations, may become limiting at apparently high levels. Animal populations generally are not capable of consuming the last food item available in a given system. Until we can say why this is so, or how far short of complete consumption arctic shorebirds actually fall, we can deal with "availability" and "limitation" only in general, not absolute terms.

In a study similar in methods to the present one, Brenner (1968) determined that Red-winged blackbirds (Agelaius phoenecius) consumed 30-70% of "available" insects. West (1967) found that the "available" seed crop in central Illinois could support far denser wintering populations of Tree sparrows (Spizella arborea) than were observed. By using such an absolute measure of availability, I could also state categorically that the tundra ecosystem could support larger breeding populations of calidridine sandpipers.

Additional evidence for short term energy limitation might be seen in a comparison of nesting C. bairdii adult weights in different seasons (Fig. 5). MacLean (1969) showed that adult bairdii are bare-ground-

Figure 5. Frequency distribution, by 2-g intervals, of observed live body weights among nesting adult bairdii in 1969 compared to other seasons.



feeding specialists, therefore deriving a large share of their requirements from adult arthropods. The exceptionally cold season of 1969 at Barrow must have so reduced surface prey mobility, hence functional availability (but not necessarily absolute availability) that these birds were mobilizing energy faster than it could be secured. The relatively slow growth rate of Calidris chicks in 1969 (Norton, 1973c) further emphasizes the overriding significance of weather-mediated resource limitation in arctic systems.

Based on our current, recently developed understanding of the trophic relationships among consumers at Barrow, we could expect to learn more about proximate limiting effects of resources. For example, the Brown lemming population "highs" at irregular intervals at Barrow should transfer a large pulse of vegetation to organic litter, which can then be used by the saprovore-based insect community (MacLean and Pitelka, 1971). This pulse should be reflected several years later by increased insect biomass, and the degree to which calidridine sandpiper population densities vary with such an input should be instructive. Similarly, we should look carefully for changes in breeding densities and reproductive success of alpina in each season following high densities of C. melanotos at Barrow. Theoretically, melanotos and alpina should be the species-pair most likely to affect each other's food resources (Holmes and Pitelka, 1968; MacLean, 1969; Norton, 1973a).

Yet another promising line of inquiry is the following of identifiable cohorts of larval tipulid insects by soil sampling at intervals, to measure the reduction in numbers as each group becomes susceptible

to avian predation. The estimates of numbers removed may be compared to the present estimates for numbers required.

Pitelka et al. (MS) regard calidridine social systems as adaptive resource exploitation strategies. Can judgment by rendered on that hypothesis in light of this discussion of energy requirements? This question can be separated into several sub-questions pertinent to particular aspects of the organization of breeding effort through space and time. The first, most basic question surrounds the origins of the dichotomy between conservative and opportunistic systems. I have argued elsewhere (Norton, 1973a) that opportunism in this group represents a fundamental and adaptive loss of site attachment that permits an annual habitat avoidance-capitalization choice. As such, an observer at one locality, as at Barrow, sees only occasionally the annual result of the choice, not the factors -- energetics included -- which may govern the choice made at other locations. Fluctuations in numbers of melanotos and of the probably opportunistic bairdii may represent the response of the populations to factors elsewhere so absolute and compelling (such as snow-covered habitat) that it is unnecessary to invoke the energetic subtleties of the situation. However, energetic subtleties and specializations seem to develop in consequence of the opportunistic approach. The increased reliance on fat investigated by MacLean (1969), and the maximized metabolic scope (Norton, 1973b) in opportunistic melanotos may be considered in this light.

Another question concerns dispersal of these birds over available habitat within a given season and at a particular locality. Spacing

mechanisms, typified by the large, exclusive nesting and feeding territories maintained by alpina at Barrow may or may not have evolved to spread birds in relation to available food resources (cf. Schoener, 1968; Holmes, 1970). Since the territorial system weakens and disappears by the time chicks hatch, spacing machanisms do not directly affect survival of post-hatching sandpipers. Holmes (1970) therefore concluded that the exclusivity proffered by territoriality could only protect the energy resources of courting, laying, and incubating adults. The energy requirements of both adults during courtship and egg-laying were indeed shown to be maximal (Fig. 1). (MacLean, MS) shows, however, that the resource in critically short supply may not be energy per se, so much as the availability of calcium for females producing eggs. I have observed that the upland tundra sites on which alpina preferentially court and establish territories at Barrow, are more likely to include raised perches used by owls and jaegers when lemmings are abundant. Around these perches, one finds casts and disintegrated casts containing lemming teeth and bones, which items appear in stomachs of laying females (MacLean, MS). Whatever the original selective advantages for territoriality, calcium balance at Barrow may influence the choice of nesting sites by alpina, and therefore be related indirectly to the extent of territory defended.

Another problem with viewing territory size as reflecting food density is that alpina territories at Kolomak River are not the site of all feeding, although prey densities are higher than at Barrow (Holmes, 1970). Moreover, we might continue to wonder whether spacing

mechanisms do not in fact evolve and function as means to reduce nest predation, in view of the low nest loss among alpina at Barrow, relative both to that of other sympatric species (Norton, 1973a) and relative to the alpina at Kolomak River (Holmes, 1970). This function of territory has been suggested previously by Hinde (1956), Tinbergen (1957), and Lack (1966), and specifically for Calidris systems by Pitelka et al. (MS).

The third question applies to an opportunistic trait which is shared by several monogamous and otherwise conservative calidridine species. How much is food consumption reduced by the departure of one adult at hatching in bairdii, melanotos , and pusilla? This feature of many species' social systems can be considered in relation to its possible adaptive value for survival of young, as suggested by Pitelka et al. (MS). There are eight adult members of the Calidris community at Barrow up to the point of hatching (i.e. two sexes in four species). At hatching, the number drops to 5, so this maximally represents a 37.5% reduction in daily adult food consumption (assuming equal population densities and energy requirements by all species). This is an impressive theoretical reduction in consumption rate, but there are reasons why this estimate is of strictly limited general significance. First, it expresses a community reduction in consumption rate, and unless we view the community as the unit of evolution, its level is a function of the more or less accidental assemblage of Calidris species populations at Barrow. The reduction of adult consumption rate in a single-species population might be either 0, or about 50%. The second reason for

treating the 37.5% figure with caution is that any estimate of reduction may overstate the actual degree of overlap between adult and chick diets. The smallest chicks, at their earliest and most critical feeding stages may be taking items such as Collembola, spiders, chironomid adults, etc., the caloric values of which may not justify the effort of feeding by the adult. In viewing the whole system whereby one adult departs Barrow, we must recognize a balancing of the effects of the adult's presence on chick survival and predation (attraction of predators vs. alarm signal capacity, affording of brooding) against those of reducing competition for resources.

The reduction of competitive resource use within species as a result of one adult's departure may be strongly selected for, if there is indeed appreciable overlap in diet items between adults and young of the same species. As chicks grow larger, the degree of overlap between adult and chick diets presumably increases. Yet, more importantly, the dissolution of the pairbond, whenever it occurs, must prevent inter-adult competition for resources in the vicinity of the brood. The brood group clearly circumscribes the arena of feeding by the attendant adults. In reference to Figure 4, we may consider that the continued consumption by two adults in such a small area might decrease the probability of either adult's achieving the required prey capture frequency, or may increase the adults' time spent feeding up to twofold. Particularly during cold weather, this increased time feeding might interfere with brooding. In this regard, the behavior of brooding alpina adults at Barrow would bear closer examination. I am

not certain whether both adults remain continuously close to the brood up to the point of fledging. If they do, then the long distances apparently travelled by the family groups even at a very early age (Holmes, 1966a; Norton, 1973a) may functionally provide the adults with a continually renewed feeding area, thereby reducing the problem of resource division between the two adults.

All of the foregoing discussion is intended as the beginning of our understanding the ecological energetics of arctic sandpipers, and not the end, that I once naively envisioned it would be. If this study proves to be such a beginning, then succeeding investigators (and those interested enough to have read this far) deserve my self-critical remarks and a brief reflection on the current state of the art. First, there are serious gaps in the data available. Digestive efficiencies, chick mortality, timed activity observations over the 24-hr cycle, efficiency of egg production -- all had to be covered by more or less educated assumptions. Secondly, future respiratory metabolism measurements on these birds should be discouraged unless the instrumentation is orders of magnitude more precise, and permits more manipulations of experimental subjects, than the system I used. Failing this capability, the effort and expense of stationing an investigator in the arctic would be wasted. Finally, the elucidation of energetic relationships of these birds will not necessarily explain all the remaining mysteries of their breeding biology. On the other hand, as begun, the study of energetics promises to generate the questions which may bring us closer to this understanding at an optimal rate.

## REFERENCES


Armstrong, E.A. 1954. The behaviour of birds in continuous daylight. Ibis 96:1-30.

Baerends, G.P. and R.H. Drent (eds.). 1970. The Herring Gull and its egg. Behaviour, Suppl. 17. Brill, Leiden.

Bernstein, M.H. 1973. Development of thermoregulation in Painted Quail, Excalfactoria chinensis. Comp. Biochem. Physiol. 44A: 355-366.

Blackmore, F.H. 1969. The effect of temperature, photoperiod and molt on the energy requirements of the House Sparrow, Passer domesticus. Comp. Biochem. Physiol. 30:433-444.

Breitenbach, R.P. and T.S. Baskett. 1967. Ontogeny of thermoregulation in the Mourning Dove. Physiol. Zool. 40:207-217.

Brenner, F.J. 1968. Energy flow in two breeding populations of Redwinged Blackbirds. Am. Midl. Nat. 79:289-310.

Brody, S. 1945. Bioenergetics and Growth. New York, Reinhold.

Brown, J. 1968. Environmental setting, Barrow, Alaska. U.S. Army Cold Reg. Res. and Eng. Lab. Unpubl. tech. note.

Brown, J. 1972. Introduction to: Structure and function of the tundra ecosystem. U.S. IBP 1971 Progress Report: 9-14.

Burley, V.E. 1968. Incubation at low temperatures by the Zebra Finch. Condor 70:184.

Calder, W.A. 1972. Heat loss from small birds: analogy with Ohm's law and a re-examination of the "Newtonian Model". Comp. Biochem. Physiol. 43A:13-20.

Cullen, J.M. 1954. The diurnal rhythm of birds in the arctic summer. Ibis 96:31-46.

Drent, R.H. 1967. Functional aspects of incubation in the Herring Gull (Larus argentatus). Brill, Leiden. (Also reprinted in Baerends and Drent, 1970).

Drent, R.H., K. Postuma and T. Joustra. 1970. The effect of egg temperature on incubation behaviour in the Herring Gull. In Baerends and Drent (1970).

Drent, R.H. MS. Adaptive aspects of the physiology of incubation. (Proc. Int. Ornith. Congr.)

Dunbar, M.J. 1968. Ecological development in polar regions. Prentice-Hall, Englewood Cliffs.

Dyer, M.I. 1968. Respiratory metabolism studies on Red-winged Blackbird nestlings. Can. J. Zool. 46:223-233.

El-Wailly, A.J. 1966. Energy requirements for egg-laying and incubation in the Zebra Finch, Taeniopygia castanotis. Condor 68:582-594.

Franks, E.C. 1967. The responses of incubating Ringed Turtle Doves (Streptopelia risoria) to manipulated egg temperatures. Condor 69:268-276.

Gessaman, J.A. 1972. Bioenergetics of the Snowy Owl (Nyctea scandiaca). J. Arctic Alpine Research 4:223-238.

Hart, J.S. and O. Heroux. 1955. Exercise and temperature regulation in lemmings and rabbits. Can. J. Biochem. Physiol. 33:428-435.

Hays, H. 1973. Polyandry in the Spotted Sandpiper, Actitis macularia. Living Bird 11 (in press).

Heldt, R., Sr. 1966. Zur Brutbiologie des Alpenstrandläufers, Calidris alpina schinzii. Corax 1(17):173-188.

Heppner, Frank. 1970. The metabolic significance of differential absorption of radiant energy by black and white birds. Condor 72:50-59.

Herreid, C.F., II, and B. Kessel. 1967. Thermal conductance in birds and mammals. Comp. Biochem. Physiol. 21:405-414.

Hilden, O. 1965. Zur Brutbiologie des Temminkstrandläufers, Calidris temminckii (Leisl.). Ornis Fenn. 42:1-5.

Hinde, R.A. 1956. The biological significance of the territories of birds. Ibis 98:340-369.

Holmes, R.T. 1966a. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (Calidris alpina) in northern Alaska. Condor 68:3-46.

Holmes, R.T. 1966b. Feeding ecology of the Red-backed Sandpiper (Calidris alpina) in arctic Alaska. Ecology 47:32-45.

Holmes, R.T. 1966c. Molt cycle of the Red-backed Sandpiper (Calidris alpina) in western North America. Auk 83:517-533.

Holmes, R.T. 1970. Differences in population density, territoriality and food supply of dunlin on arctic and subarctic tundra. In A. Watson (ed.) Animal populations in relation their food resources. Brit. Ecol. Soc. Symp. 10 (Blackwell, London): 303-322.

Holmes, R.T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (Calidris alpina). Condor 73:93-99.

Holmes, R.T. and F.A. Pitelka. 1964. Breeding behavior and taxonomic relationships of the Curlew Sandpiper. Auk 81:362-379.

Holmes, R.T. and F.A. Pitelka. 1968. Food overlaps among coexisting sandpipers in northern Alaska tundra. Syst. Zool. 17:305-318.

Hooper, E.T. and M. El Hilali. 1972. Temperature regulation and habits of two species of jerboa, genus Jaculus. J. Mammal. 53:574-593.

Irving, L. 1960. Birds of Anaktuvuk Pass, Kobuk, and Old Crow. U.S. Nat. Mus. Bull. 217:viii + 409 pp.

Irving, L. and J. Krog. 1955. Temperature of skin in the arctic as as regulator of heat. J. Appl. Physiol. 7:355-364.

Kahl, P.M. 1962. Bioenergetics of growth in nestling Wood Storks. Condor 64:169-183.

Kelley, J.J., Jr. and D.F. Weaver. 1969. Physical processes at the surface of the arctic tundra. Arctic 22:425-437.

Kendeigh, S.C. 1949. Effect of temperature and season on energy resources of the English Sparrow. Auk 66:113-127.

Kendeigh, S.C. 1952. Parental care and its evolution in birds. Illinois Biol. Monogr. 22:1-358.

Kendeigh, S.C. 1963. Thermodynamics of incubation in the House Wren, Troglodytes aedon. Proc. XIII Int. Orn. Congr. (1962): 884-904.

Kendeigh, S.C. 1969a. Tolerance of cold and Bergman's Rule. Auk 86: 13-25.

Kendeigh, S.C. 1969b. Energy responses of birds to their thermal environments. Wilson Bull. 81:441-449.

King, J.R. and D.S. Farner. 1961. Energy metabolism, thermoregulation, and body temperature. In A.J. Marshall (ed.) Biolgy and Comparative Physiology of Birds. New York, Academic Press: 215-288.

Kleiber, M. and J.E. Dougherty. 1934. The influence of environmental temperature on the utilization of food energy in baby chicks. J. Gen. Physiol. 17:301-726.

Kleiber, M. 1961. The Fire of LIfe. New York, Wiley. 454 pp.

Kontogiannis, J.E. 1968. Effect of temperature and exercise on energy intake and body weight of the white-throated sparrow Zonotrichia albridlis. Physiol. Zool. 41:54-64.

Koskimies, J. 1962. Ontogeny of thermoregulation and energy metabolism in some gallinaceous birds. Suppl. Ricierche Zool. Appl. alla Caccia 4:149-160.

Lack, D. 1966. Population studies of birds. Clarendon, Oxford.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lasiewski, R.C. 1963. Oxygen consumption of torpid, resting, active, and flying humming birds. Physiol. Zool. 36:122-140.

Lennerstedt, I. 1966. Egg temperature and incubation rhythm of a Capercaillie (Tetrao urogallus L.) in Swedish Lapland. Oikos 17: 169-174.

MacLean, S.F., Jr. 1969. Ecological determinants of species diversity in arctic sandpipers near Barrow, Alaska. Unpubl. Ph.D. thesis, Univ. of California, Berkeley.

MacLean, S.F., Jr. 1970. Arthropod Populations. In J. Brown and G.C. West (eds.) Tundra Biome Research in Alaska. U.S. IBP Tundra Biome Report 1970-1, 44-48.

MacLean, S.F., Jr. 1971. Population ecology and energetics of tundra soil arthropods. In J. Brown and S. Bowen (eds.) The structure and function of the tundra ecosystem. U.S. IBP Tundra Biome 1971 Progress Report, vol. I: 126-130.

MacLean, S.F., Jr. 1972. A simulation model to predict the habitat distribution of shorebird feeding activity. Proc. Tundra Biome Symposium: 149-154.

MacLean, S.F., Jr. MS. Life cycle of Pedicia hannai antennata Alex. (Diptera: Tipulidae) -- an arctic crane fly. (Oikos, 1973).

MacLean, S.F., Jr. MS. Small mammal bones and teeth in the diet of arctic sandpipers. (Ibis, 1973)

MacLean, S.F., Jr. and R. T. Holmes. 1971. Bill lengths, wintering areas, and taxonomy of North American Dunlins, Calidris alpina. Auk 88:893-901.

MacLean, S.F., Jr. and F.A. Pitelka. 1971. Seasonal patterns of abundance of tundra arthropods near Barrow, Alaska. Arctic 24: 19-40.

MacMullen, R.A. and L.L. Eberhardt. 1953. Tolerance of incubating pheasant eggs to exposure. J. Wildlife Management 17:322-330.

Maher, W.J. 1964. Growth rate and development of endothermy in the Snow Bunting (Plectrophenax nivalis) and Lapland Longspurs (Calcarius lapponicus) at Barrow, Alaska. Ecol. 45:520-528.

Mertens, J.A.L. 1967. The influence of brood size on the energy metabolism and water loss of nestling Great Tits, Parus major major. Ibis 111:11-16.

Miller, L.K. 1967. Caudal nerve function as related to temperature in some Alaskan mammals. Comp. Biochem. Physiol. 21:679-686.

Miller, L.K. and L. Irving. 1967. Temperature-related nerve function in warm- and cold-climate muskrats. Am. J. Physiol. 213: 1295-1298.

Mullen, R.K. 1971. Energy metabolism and body water turnover rates of two species of free-living Kangaroo rats, Dipodomys merriami and Dipodomys microps. Comp. Biochem. Physiol. 39A:379-390.

Norton, D.W. 1970a. Thermal regime of nests and bioenergetics of chick growth in the Dunlin (Calidris alpina) at Barrow, Alaska. Unpubl. Master's thesis, Univ. of Alaska, College.

Norton, D.W. 1970b. Avian populations and production, p. 48-49. In J. Brown and G.C. West (eds.) Tundra Biome Report 70-1.

Norton, D.W. 1971. Two Soviet recoveries of Dunlins banded at Point Barrow, Alaska. Auk 88:927.

Norton, D.W. 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. Condor 74:164-176.

Norton, D.W. 1973a. Phenology, breeding densities, nesting success, and other vital statistics for four species of calidridine sandpipers breeding at Barrow, Alaska. Unpubl. Ph.D. thesis, Univ. of Alaska, Fairbanks: Chapter 1.

Norton, D.W. 1973b. Respiratory metabolism and energy budget during the nesting period in calidridine sandpipers at Barrow, Alaska. Unpubl. Ph.D. thesis, Univ. of Alaska, Fairbanks: Chapter 3.

Norton, D.W. 1973c. Bioenergetics, thermoregulation, and growth of calidridine sandpiper chicks at Barrow, Alaska. Unpubl. Ph.D. thesis, Univ. of Alaska, Fairbanks: Chapter 4.

Norton, D.W. 1973d. Synthesis: ecological energetics of calidridine sandpipers breeding at Barrow, Alaska. Unpubl. Ph.D. thesis, Univ. of Alaska, Fairbanks: Chapter 5.

Norton, D.W. MS. Embryonic cold exposure, hatching synchrony, and chick viability among arctic calidridine sandpipers.

Obaldiston, G.W. 1966. The response of the immature chicken to ambient temperature. In: C. Horton-Smith and E.C. Amoroso (eds.) Physiology of the domestic fowl. London, Oliver and Boyd: 228-234.

Oppenheim, R.W. 1968. Light responsivity in chick and duck embryos just prior to hatching. Anim. Behav. 16:276-280.

Oring, L.W. 1972. Monogamy and polyandry in the Spotted Sandpiper. Abstr. 90th annual A.O.U. Meeting, August 1972: p. 21.

Parmelee, D.F. 1970. Breeding behavior of the Sanderling in the Canadian high arctic. Living Bird 10:97-146.

Phillipson, J. 1966. Ecological energetics. Arnold, London. 57 pp.

Pitelka, F.A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61:233-264.

Pitelka, F.A., R.T. Holmes, and S.F. MacLean, Jr. MS. Ecology and evolution of social organization in arctic sandpipers. (Am. Zool. 1973).

Pitelka, F.A., P.Q. Tomich, and G.W. Treichel. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecol. Monogr. 25:85-117.

Pohl. H. 1969. Some factors influencing the metabolic response to cold in birds. Fed. Am. Soc. Exp. Biol. Proc. 28:1059-1064.

Pohl, H. and G.C. West. In press. Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the Common Redpoll. (Comp. Biochem. Physiol. 44A).

Renner, M. 1960. The contribution of the honey bee to the study of time-sense and astronomical orientation. Cold Springs Harbor Symp. Quant. Biol. 25:361-367.

Romijn, C. and W. Lockhorst. 1956. The caloric equilibrium of the chicken embryo. Poultry Sci. 35:829-834.

Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits, Parus major. Ibis 108:313-347.

Safriel, U.N. 1971. Population study of the Semipalmated Sandpiper, Calidris pusilla. 1971 AAAS Metgs, Alaska. Proc. 22nd Alaska Sci. Conf.: 35.

Schoener, T.W. 1968. Sizes of feeding territories among birds. Ecol. 49:123-141.

Serventy, D.I., D.S. Farner, C.A. Nichols, and N.E. Stewart. 1962. Trapping and maintaining shorebirds in captivity. Bird-Banding 33:123-130.

Skutch, A.F. 1962. The constancy of incubation. Wilson Bull. 74: 115-152.

Soikkeli, M. 1967. Breeding cycle and population dynamics in the Dunlin (Calidris alpina). Ann. Zool. Fenn. 4:158-198.

South, F.E. and W.A. House. 1967. Energy metabolism in hibernation. In K.C. Fisher (ed.) Mammalian hibernation III, 1967, New York, Amer. Elsevier: 305-324.

Theberge, J. B. and G. C. West. MS. Significance of brooding to the energy demands of Alaskan Rock Ptarmigan chicks. (Arctic, 1973).

Tinbergen, N. 1957. The functions of territory. Bird Study 4:14-27.

Tucker, W.A. 1968. Respiratory exchange and evaporative water loss in flying budgerigars. J. Exp. Biol. 48:67-87.

Vince, M.A. 1966. Artificial acceleration of hatching in quail embryos. Anim. Behav. 14:389-394.

Vince, M.A. 1968. Retardation as a factor in the synchronization of hatching. Anim. Behav. 16:332-335.

Von Haartman, L. 1956. Der Einfluss der Temperatur auf den Brut-rhythmus experimentell nachgewiesen. Ornis Fenn. 33:100-107.

Weeden, J.S. 1966. Diurnal rhythm of attentiveness of incubating female Tree Sparrows (Spizella arborea) at a northern latitude. Auk 83:368-388.

Weller, G. and C. Benson. 1971. The micro- and regional climate of the Alaskan arctic tundra. U.S. IBP Tundra Biome 1971 Progress Report: 181-193.

Watson, A. and R. Moss. 1970. Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. In A. Watson (ed.) Animal populations in relation to their food resources. Brit. Ecol. Soc. Symp. 10. (Blackwell, London): 167-220.

West, G.C. 1960. Seasonal variation in the energy balance of the Tree Sparrow in relation to migration. Auk 77:306-329.

West, G.C. 1967. Nutrition of tree sparrows during winter in central Illinois. Ecol. 48:58-67.

West, G.C. 1968. Bioenergetics of captive Willow Ptarmigan under natural conditions. Ecol. 49:1035-1045.

West, G.C. 1972. The effect of acclimation and acclimatization on the resting metabolic rate of the Common Redpoll. Comp. Biochem. Physiol. 42A:293-310.

West, G.C. 1973. Foods eaten by tree sparrows in relation to availability during summer in northern Manitoba. Arctic, in press.

West, G. C. and B. DeWolfe. MS. Populations and energetics of taiga birds near Fairbanks, Alaska.

Wiegert, R.G. 1968. Thermodynamic considerations in animal nutrition. Am. Zool. 8:71-81.